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A TEXT-BOOK

OF

INVERTEBRATE MORPHOLOGY

BY

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PREFACE.

THE Morphology of Invertebrate Animals may be treated either from the standpoint of Comparative Anatomy or from the zoölogical side, and either method of treatment has much to recommend it. In my experience, however, the zoölogical method has proved most satisfactory for the presentation of the subject to students, inasmuch as it is necessarily the method employed in the laboratory, and accordingly in the present work that plan of presenting the facts of morphology has been followed. A bare statement of the structural peculiarities of the various groups, however, is simply collecting the bricks and stones without the mortar necessary to unite them together into a substantial edifice, and where the opportunity has presented itself attention has been directed to the comparative significance of various organs and to the affinities of the various groups.

A word is perhaps necessary in regard to the classification adopted, which presents many radical changes from the schemes usually employed. For the larger groups, following the example of Claus, the term *type* has been employed, and no less than twelve of these types are adopted. This increased number has resulted from a division of two groups usually recognized, namely, the Vermes and the Arthropoda. As regards the former it has long been acknowledged to be a heterogeneous collection, and its retention is to be regarded as a survival. It is true that the forms assigned to it do present certain phylogenetic affinities; but if this is to be the reason for its retention, then the Mollusca and Prosopygia (Molluscoidea) should also be assigned to it. It has seemed more satisfactory to retain the Mollusca and Prosopygia as distinct groups, and to divide the Vermes into several types, such as the Platyhelminthes, Nemathelminthes, and Annelida, each of the same rank as the Mollusca, and presenting approximately similar degrees of affinity among themselves.

As to the Arthropoda, its right to exist as a group coördinate with, for instance, the Mollusca has been questioned by several authors. Undoubtedly in this case also many similar structural features obtain among the various members of the group, but embryology has indicated a probability of a more or less independent origin of two Arthropodan groups usually regarded as closely related, namely, the Arachnida and the Tracheata proper. Apparently the former have originated from Crustacean ancestors, while, if the supposed significance of *Peripatus* be accepted, the Tracheates are to be traced back to Annelidan forebears, and for the purpose of calling the attention of the student to this probable phylogeny the Crustacea, Arachnida and Tracheata have been regarded as distinct types coördinate with the Annelida and Mollusca.

A book of this kind must necessarily be highly tinged with the individual opinions of the writer, and for these indulgence must be craved. So far as the facts are concerned every care has been taken that they should be accurate and as far as possible up to date with the most recent investigations. Errors have no doubt crept in, a misfortune almost inevitable from the mass of material which must pass under consideration during the progress of the work, and for these again indulgence must be asked.

Refraining from further apologies, the more pleasant duty remains of thanking the many friends who have so kindly aided the work by suggestion or otherwise, and especially those who have permitted the use of figures taken from special papers. A large number of the figures employed are original and the great majority have been especially drawn for this work, the attempt being made to diagrammatize them to a greater or less extent for the sake of clearness. In all cases where figures have been borrowed the original authorship has been duly acknowledged.

Finally, I desire to make public recognition of my indebtedness to my wife for the invaluable assistance she has rendered in many ways during the progress of the work.

J. PLAYFAIR McMURRICH.

UNIVERSITY OF MICHIGAN,
September, 1894.

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INVERTEBRATE MORPHOLOGY.

CHAPTER I.

PROTOPLASM AND THE CELL.

In the examination of organisms presenting the series of phenomena which we term life, the invariable presence of a peculiar semi-fluid transparent or hyaline substance becomes quickly apparent. Whether the organism be a plant or an animal, whether it be of the simplest or of the most complex organization, it is still composed of this substance, which is known as *protoplasm*, and it may be said that so far as our knowledge extends life never exists except in association with this material. Protoplasm is "the physical basis of Life," and it becomes of great importance that its nature should be fully understood, in order that the results of its activities, Life, may become more intelligible.

Much has yet to be accomplished, however, before an accurate knowledge of the structural and chemical characters of this substance is obtained, and indeed it is incorrect to regard it as a substance, since it is rather the aggregate of a large number of exceedingly complex chemical compounds, none of which are sufficiently known. From the very nature of things it is impossible at present to get a correct idea of these substances and the relations which they bear to one another, since our present analytical methods are not capable of determining and isolating them in living protoplasm and the mere act of subjecting protoplasm to analysis destroys those very relationships which are the cause of the vital manifestations.

Dead protoplasm is something very different from living protoplasm, and our present knowledge only imperfectly extends to this much-altered material.

Furthermore even in the dead material the chemist has to deal not only with the complex substances which constitute protoplasm proper, but also with numerous secondary products either in the process of being built up into protoplasmic molecules or else resulting from the destruction of these molecules. For both these processes are continually going on, the living organism continually uniting simple chemical compounds to form new complex molecules, a process known as anabolism, and resulting in growth; and just as continually it is resolving into simpler compounds the complex molecules already formed, a process known as catabolism, and resulting in the manifestation of energy in its various forms, such as heat, motion, electricity, and even light. Growth and the manifestation of energy are then two most important phenomena exhibited by living organisms, standing in opposition to one another and determining the general condition of the organism. If anabolic changes are the more active, then the animal or plant grows, as we express it, adds new protoplasm and increases in size; if the anabolic and catabolic changes are practically equal in amount, stability results; while the preponderance of catabolism leads to a lessening of material, and finally to what we term death. These changes constitute a cycle occurring in the life-history of probably every organism and causing the periods which we denote as youth, maturity, and old age.

Dead protoplasm then, together with the anabolic and catabolic constituents which are inextricably associated with it, will be found on analysis to consist to a large extent of the chemical elements Carbon, Hydrogen, Oxygen, and Nitrogen, together with Sulphur and Phosphorus, as well as a number of substances present in varying amounts, such as Chlorine, Potassium, Sodium, Iron, Calcium, and Magnesium. Exactly how these various elements are united together it is difficult to determine, but especial importance has been assigned to the C, H, O, N, and S compounds which occur and which form a group of chemical compounds known as Proteids. Of such compounds several, such as Albumin, Globulin, Fibrin, Plastin, Nuclein, have been isolated from protoplasm, some being probably secondary products resulting from the alteration of the protoplasmic molecules proper, but others, such as Plastin and Nuclein, are especially constant, and seem to be important constituents of the protoplasmic complex.

Plastin forms when isolated a sticky fibrous mass, insoluble in concentrated alkaline solutions and unaffected by the peptic and tryptic ferments, and consists of C, H, O, N, S, and P. Nuclein is more especially characteristic of a special portion or modification of protoplasm termed the nucleus, of which more will be said hereafter, and resembles plastin very closely, being, however, less insoluble than it, and consists of the same chemical elements. Analyses of these substances, however, differ greatly, the nuclein from spermatozoa, for instance, containing no sulphur; and it seems probable not only that they differ materially according to the source from which they are obtained, but also that they are not really chemical compounds, but a mixture of several highly complex substances.

With these proteids, then, there exist in protoplasm various salts, such as Potassium, Sodium, and Calcium phosphate, Potassium and Sodium chloride, Magnesium sulphate, and other such salts, the exact significance of which it is difficult to estimate. How living protoplasm differs chemically from dead has not up to the present been accurately determined.

As regards its general structure protoplasm appears as a moderately consistent jelly-like substance, usually colorless and more or less granular in appearance. As a rule the peripheral portion of a mass of protoplasm is less granular than the central, appearing therefore clearer, and is especially distinguished as the ectoplasm from the more opaque endoplasm. Imbedded in the endoplasm are to be found usually various bodies, the products of the activities of the protoplasm, such as large, clear spaces occupied by fluid and known as vacuoles, food-particles of various kinds in the simpler organisms, starch granules and crystals in plant-protoplasm, and depositions of pigment. One particular structure, the nucleus, however, seems to be invariably present, occupying the central portion of the mass, and, as will be seen later, playing a very important rôle in the life of the protoplasm. It is indeed a specially modified portion of the protoplasm and cannot, therefore, be placed in the same category as the vacuoles and other accidental or secondary constituents which have been mentioned, and every mass of protoplasm may be considered as consisting of two essential parts, the protoplasm proper or *cytoplasm* and the special modification of it, the nucleus, which for convenience is termed the *caryoplasm*. Such a combination of cytoplasm and caryoplasm forms what is technically known as a *cell*, and all living organisms are composed of one or more such structures, which are to be regarded therefore as morphological units.

If the more intimate structure of the cytoplasm of such a unit or cell (Fig. 1) be examined, disregarding the various secondary constituents it may enclose, it will be found to consist of a network of exceedingly fine fibrils, along which, and more especially at the points where two or more of them meet, are to be found minute granules which stain deeply with the ordinary microscopical staining reagents. The fibrils constitute the *reticulum* (Fig. 1, *r*) of the cytoplasm, and the granules are termed the *microsomes* (*m*). The reticulum seems to be formed principally of the proteid substance already mentioned as plastin, and its meshes are occupied by a more fluid substance which has been termed the *cytolymph* (*cl*).

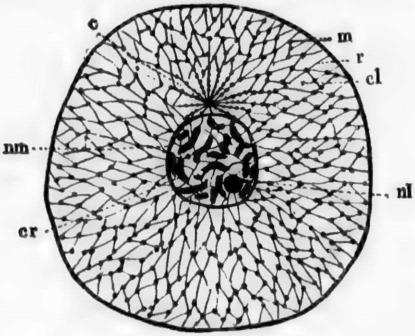

Fig. 1.—Diagram showing the Structure of an Animal Cell.

c = centrosome. *m* = microsome.
cl = cytolymph. *nl* = nucleolus.
cr = chromatin. *nm* = nuclear membrane.
r = reticulum.

Several opinions have been given in regard to the structure of the cytoplasm, in addition to that here presented, according to which it may be compared to a sponge the meshes of whose network are occupied by the cytolymph. According to another view it is composed of a number of fibrils of varying lengths imbedded in a matrix, the fibrils corresponding to the reticulum of the reticular theory and the matrix to the cytolymph. According to still another theory which rests on the appearance produced in the cytoplasm by a special method of treatment, there is present a colorless matrix in which are imbedded numerous exceedingly small granules sometimes scattered and sometimes united together into chains. Indeed the upholder of this granular theory has carried his view to the extent of regarding the granules as structural units of which the cell is composed, its structure being comparable to that of a zooglœa of micrococci. It seems probable, however, that the granules are to a large extent secondary products of the activities of the cytoplasm and have therefore but a subordinate value in its composition. The reticular theory seems to stand more nearly in harmony with the majority of observations, though it must be admitted that some observers do not seem to have perceived the true reticulum, confining their attention to the coarser network produced in some cases by extensive vacuolization of the cell.

An imitation of the cytoplasm has been recently obtained by the mixture of thickened olive-oil with a solution of potassium carbonate or of chloride of sodium, the watery solution taking the form of polyhedral globules each surrounded by a thin layer of oil which from its higher refractive index gives the appearance of the plastin reticulum surrounding the cytolymph. Solid particles finely divided and mixed with the oil tend to collect at the points where the oil-films of three of the globules come together, and resemble the microsomes, while it is further noticeable that under certain conditions the superficial globules of the emulsion take on a columnar form and may be compared with the ectoplasm of the cell. It is possible that the cytoplasm may have this structure, in which case the reticular theory would require to be modified, since there would no longer be a spongy structure, but rather an emulsion in which the cytolymph is divided into a number of globules each surrounded by a thin layer of plastin. At present, however, the reticular theory seems to correspond most accurately with the actual appearances, and therefore may be provisionally accepted.

The caryoplasm or nucleus, as already stated, lies usually about the middle of the cytoplasm and to a certain extent resembles it, though it presents certain peculiar features. It is usually round or oval, though occasionally it may assume elongated, horseshoe-shaped, moniliform, or even branching forms, and is as a rule clearly marked off from the cytoplasm by a membrane (Fig. 1, *mm*), which, however, at certain periods of nuclear activity seems to disappear, a new one subsequently forming. Traversing the space enclosed by the membrane, so as to form a network, are fibres which do not stain very deeply with the usual staining fluids and which are composed of a substance termed *linin*, which does not, however, appear to differ essentially from the plastin of the cytoplasm. Indeed it is not improbable that the linin network is continuous through the nuclear membrane with the plastin reticulum and that both are identical, as is also the caryolymph contained in the meshes of the linin with the cytolymph.

A more characteristic substance is the *chromatin* (Fig. 1, *cr*), so called from the strong affinities it shows for many staining fluids, such as carmine, hæmatoxylin solutions, and certain aniline stains. It seems to consist of the substance nuclein, already alluded to, and in the resting nucleus forms a reticulum intimately associated with the linin network, which it usually to a considerable extent obscures. Where the various strands of the network meet, thickenings of the chromatin sometimes occur, producing densely staining bodies (*nl*) to which the term nucleoli is given, though it is probable that bodies of a somewhat different composition are also included under this name; for there are usually to be found in the nucleus, imbedded in the substance of the network, one or more spherical bodies whose chemical reactions differ noticeably from those of the chromatin nucleoli, the substance of which they are composed being termed *paranuclein* or *pyrenin*.

There are then in the cell the following structural constituents:

- I. Cytoplasm:
  - membrane (cell-wall),
  - reticulum (plastin),
  - cytolymph.
- II. Caryoplasm:
  - membrane,
  - reticulum (linin),
  - caryolymph,
  - chromatin network (nuclein),
  - nucleoli (nuclein and paranuclein).

In addition to these there is, however, still another body to be mentioned which is especially evident in cells which are undergoing multiplication, but which has also been found in various resting cells, especially in lymph-corpuscles, various kinds of endothelial cells, and in pigment-cells. This is the structure known as the *centrosome* (Fig. 1, *c*). It is usually an exceedingly small spherical body which does not readily stain with the reagents which place the chromatin in evidence, but has a strong affinity for certain acid aniline stains, such as safranin, fuchsin, or orange. Usually but a single centrosome is present in each cell, though occasionally two or even more may occur, and it is situated in the cytoplasm in the neighborhood of the nucleus, sometimes resting in a slight concavity on the surface of that structure. Surrounding the centrosome there is frequently to be seen, more especially in dividing cells, a clear area, the archoplasm sphere, and from the periphery of this rays pass out in all directions, whence the term *aster* which is applied to the combination of the centrosome, archoplasm and the cytoplasmic rays. (See Fig. 2 *bis*.)

The significance of the centrosome will be seen later when the phenomena of cell-division are under consideration, but its origin may be inquired into at this place. Two views are current in regard to this matter, according to one of which the centrosome has its origin in the nucleus and at a certain period of the cell's existence is extruded from it. In favor of this view the intimate association of the centrosome and the nucleus are pointed out, an association which becomes especially pronounced during cell-division, the astral rays connected with the centrosome appearing to penetrate the nucleus and in fact to bring about its division into two parts. According to the other theory, however, the centrosome is a constituent of the cytoplasm and in its origin has nothing to do with the nucleus. Quite recently an interesting amplification of this idea has been suggested to the effect that the centrosome is nothing more or less than an aggregation of cytoplasmic microsomes. The astral rays are cytoplasmic fibres converging from all sides, and since microsomes occur along their course an aggregation of these bodies might be found where the fibres meet. This idea cannot be discussed in detail here, but it may be pointed out that the absence of a centrosome in cells which have lost their powers of reproduction is readily explicable on this idea, the aggregated microsomes having scattered in such cells, and furthermore that the theory explains certain peculiar arrangements replacing the typical aster during the division of some cells.

Such a combination of cytoplasm and caryoplasm constitutes a morphological element capable of carrying on all the functions of life. It is not only a morphological but also a physiological element. It is capable of assimilating the necessary substances and building up protoplasm; metabolism and the consequent evolution of energy goes on in it; it excretes waste products; it is contractile and may therefore be capable of motion; it responds to stimuli of various kinds, or in other words it is irritable; and, finally, it is capable of reproduction. The question naturally arises, however, whether this combination of the two substances mentioned is essential—whether, that is to say, organisms without nuclei do not exist and manifest all the phenomena of life. At one time the existence of unicellular organisms destitute of a nucleus was recognized, the term *cytode* being applied to them to distinguish them from nucleated cells. Within recent years, however, a growing skepticism has come into existence as to the non-nucleate character of these organisms, the recent improvements of the microscope and the application of modern staining reagents having revealed the existence of nuclei in many of the forms at one time regarded as typical cytodes. It would perhaps be going too far to state that cytodes do not exist, but the evidence at hand indicates that their existence is highly problematical.

This conclusion is strengthened by the results which have been obtained from the observations of artificially produced cytodes. Some of the larger unicellular organisms have been cut into fragments some of which can be definitely shown to be destitute of nuclear or caryoplasmatic substance. In such cases it is found that the nucleated fragments if placed under proper conditions will regenerate and carry on their existence as before, while the cytode fragments, though manifesting signs of life for a considerable length of time, will not regenerate and do not possess the power of reproduction. The nucleus seems to possess a marked regulating or coördinating action upon the cytoplasm, coördinating the anabolic and catabolic activities upon which the continuance of life depends.

It would be beyond the scope of the present work to enter into a discussion of the various forms of physiological activity of the cell, but one of its physiological functions, reproduction, must receive special attention in connection with the remarkable structural changes which accompany it. Since the disproval of the doctrine of spontaneous generation the epigrammatic statement *Omnis cellula e cellulâ* has been the watchword of modern histology and embryology, and to-day it finds its complement in a corresponding epigram, *Omnis nucleus e nucleo*. Every cell at present in existence may be assumed to have descended from some previously existing cell, and the nucleus it contains to be a portion of the nucleus of the ancestral cell. New cells arise by the division of previously existing cells, and each division of the cytoplasm is accompanied by a division of the nucleus. Not but that under certain conditions a division of the nucleus may occur without a corresponding division of the cytoplasm, multinucleated cells thus arising, and conversely a division of the cytoplasm may possibly in certain cases be inaugurated without entailing a division of the caryoplasm; but, as might be expected from the relation which exists between the nucleus and the cytoplasm, the division of the latter is usually preceded by a division of the caryoplasm.

This latter process may take place in two ways. It may begin as a simple constriction of the nucleus which, becoming deeper and deeper, finally separates off a portion of it, a division of the cytoplasm in a similar manner then occurring, so that each of the new cells thus formed contains a portion of the original nucleus. This method of nuclear division, which is rather rare, occurs for instance in the embryonic membranes of the Scorpion and is termed *direct* or *amitotic* division, to distinguish it from the more usual *indirect* or *mitotic* method which is accompanied by a series of complicated phenomena to which the general term *karyokinesis* or *mitosis* is applied.

Starting with a typical cell, consisting of the various parts mentioned above, the karyokinetic phenomena may be regarded as affecting two constituents, i.e. the centrosome together with the surrounding archoplasm and the nuclear chromatin. The centrosome first divides, the two resulting portions gradually separating from one another (Fig. 2, *A*) until they lie at opposite poles of the nucleus, usually taking up a position ninety degrees distant from the point at which the original centrosome lay. During this process the radiating filaments which surround the centrosome become especially distinct and may be divided into two portions, those which come in contact with the nucleus and which from their appearance in later stages are termed the *spindle-fibres*, and those which radiate outwards and are lost in the cytoplasmic network and form the *aster*. In the meantime, however, important changes have been taking place within the nucleus. The chromatin substance, which originally was scattered in a reticulum, begins to arrange itself in a band (Fig. 2, *A*) which with many turns traverses the nuclear substance, the nucleoli which were present at the same time gradually vanishing. This stage of the process is termed the skein stage. The spindle-fibres of the centrosome then appear to penetrate through the nuclear membrane, which sooner or later disappears, and by their growth push the chromatin skein towards

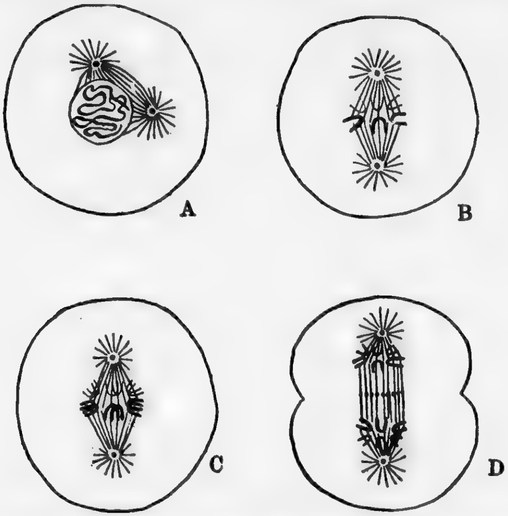

FIG. 2.—DIAGRAM SHOWING THE PHENOMENA OF CELL-DIVISION.

A, separation of the centrosomes and archoplasm; chromatin in skein-stage.
B, fully formed spindle; chromatin loops formed.
C, longitudinal division of the chromatin loops.
D, separation of chromatin loops and commencement of the division of the cytoplasm.

the equator of the nucleus, the skein at the same time breaking into a number of fragments, termed *chromosomes.* The number of these chromosomes is practically constant for the cells of any species of animal, and though there is considerable variation in different species, yet in the majority of observed cases the number belongs either to the series 2, 4, 8, 16, 32, or to that of 6, 12, 24. They vary considerably in size in different forms, being in some cases V-shaped or in others dumbbell-shaped, and arrange themselves finally in a more or less definite ring surrounding the equator of the nucleus. At this stage, which is known as the equatorial-plate stage, the appearance presented in Figure 2 *bis* is found. At each pole (*a*) of the nucleus is a centrosome (*c*) surrounded by archoplasm and by the astral rays and with the spindle-fibres extending towards and coming in contact with the chromosomes (*cr*) lying at the equator of the nucleus; to this entire complex the term *amphiaster* is sometimes applied.

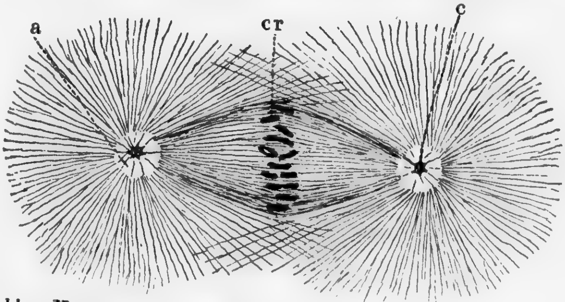

FIG. 2 *bis*.—Karyokinetic spindle from a segmenting egg of a mollusc, *Fulgur carica*. *a* = archoplasm, *c*=centrosome, *cr* = chromosomes.

In the next stage the V-shaped chromosomes, to take this as a typical shape, which are arranged with the apex of the V towards the nuclear axis, divide longitudinally. Assuming that there were originally six chromosomes in the equatorial plate, as the result of the division there are now twelve arranged in pairs (Fig. 2, *C*). One of each pair now proceeds to move towards one of the poles of the nucleus and the other to the other, so that eventually near each pole there is a group of six chromosomes, and between the two groups there may be seen stretched a number of connecting fibres identical in appearance with the original spindle-fibres, while in some cases at the equator of the egg there is to be seen on these fibres a number of darkly staining dots which may be termed the intermediate bodies (Fig. 2, *D*). At about this stage the cytoplasm begins to divide, the plane of its division passing through the equator of the nucleus, and there are thus formed two cells, each containing a nucleus composed of six chromosomes and a centrosome. The chromosomes now begin to become irregular in shape, they gradually fuse and are finally scattered in the form of a chromatic reticulum through the substance of the nucleus, which thus passes again into the resting stage, developing a new nuclear membrane.

Our knowledge of many of the details of karyokinesis is yet imperfect, and especially is this the case with regard to the mode in which the centrosome exerts its influence. It has been regarded as a simple centre of attraction, similar to the pole of a magnet, but the spindle-fibres seem to be more than passive in the phenomena. A comparison of the centrosome with an aggregation of microsomes has already been referred to, and if this idea be extended some light may be thrown upon the spindle-fibres. They would then naturally be regarded as reticular fibres, i.e. fibres of plastin to which a certain amount of contractility and extensibility may be ascribed. During the earlier stages of karyokinesis their extensibility is more manifest, and extending into the nucleus they compress its chromatic substance, the contractility manifesting itself later and determining the migration of the chromatin loops or chromosomes towards the poles of the nucleus. Furthermore, since the linin reticulum of the nucleus is probably continuous with the plastin reticulum of the cytoplasm, it is conceivable that the activities of the centrosomes may call out in it changes of contraction or extension which may suffice to bring about the characteristic skein formation of the chromatin and the subsequent fragmentation of the skein into the chromosomes, as well as the formation of the connective fibres, the intermediate bodies upon these being regarded as microsome.

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CHAPTER II.

SUBKINGDOM PROTOZOA.

A SIMPLE cell, as has already been stated, possesses the power of performing all the functions of life, and consequently the existence of unicellular organisms is possible. Such organisms, together with those which consist of a number of cells grouped together, each cell, however, retaining to a greater or less extent its own individuality, are grouped together in a subkingdom and are collectively termed PROTOZOA. In its simplest form a Protozoon may show but little differentiation of its protoplasm, but in the majority of cases various portions of the cell-substance take upon themselves special functions, and in accordance with this physiological differentiation undergo various structural modifications. Locomotor and prehensile structures of various forms may be developed, excretory pulsating vacuoles, a permanent mouth and pharynx, special contractile bands, and even pigment spots presumably connected with light absorption may occur, and in addition the power of secreting horny, calcareous, or siliceous skeletons, serving either as protective or supportive structures, is frequently present. A high degree of complexity may therefore occur in a unicellular organism, a complexity produced by a differentiation of various portions of the protoplasm composing the individual. For the most part the organisms are simple, but occasionally they associate together to form colonies. The individuals of the colonies are as a rule all alike, each carrying on all the functions of existence for itself, and there is no division of labor among the various individuals. The complexity which exists is individual and not colonial. A few forms, however, such as *Volvox*, do present a certain amount of colonial differentiation ; all the cells composing the colony are not perfectly identical physiologically, some becoming, for instance, specialized for reproductive purposes, while the rest take but little part in this process. Such a colony presents indications of a passage towards a higher grade of individuality, some of the various cell-individuals merging to a certain extent their individualities in that of the entire colony, and becoming somewhat dependent for existence on the coöperation of their fellows. This dependence, however, never reaches a high degree of development in the Protozoa and is for the most part entirely absent. It is in this respect that colonial Protozoa differ from the higher organisms, but the difference is one of degree, not of kind.

Four well-marked classes may be distinguished among the Protozoa:

I. Cl. Rhizopoda.
II. Cl. Sporozoa.
III. Cl. Flagellata.
IV. Cl. Infusoria.

I. CLASS **RHIZOPODA.**

The simplest Rhizopods present an approach to the least complicated condition under which protoplasm is known to us. They are simply small masses of protoplasm, more or less granular towards the centre, clearer towards the periphery, and continually alter their shape by pushing out lobe- or thread-like processes known as *pseudopodia* (Fig. 3, *ps*).

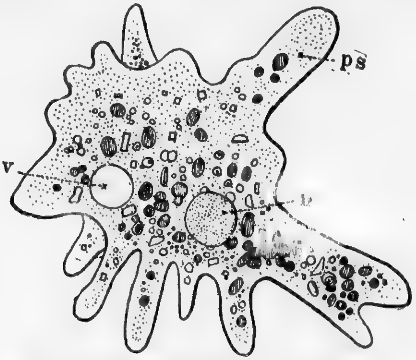

FIG. 3.—*Amœba proteus* (after GRÜBER).

cv = contractile vacuole.
n = nucleus.
ps = pseudopodium.

By throwing out such a process and flowing after it, as it were, locomotion is performed, which from a well-known genus of the class is termed *amœboid*. Food is simply engulfed by the protoplasm flowing around it, after it has come in contact with a pseudopodium, and the digestion of the food-substance takes place within the protoplasm, being thus intracellular. Undigestible material is discarded at any part of the body; respiration and excretion are carried on by the general surface; and reproduction is limited to the simple process of division.

It is rare, however, to find such a simple condition as this; even among the simpler forms a certain differentiation of the protoplasm exists, and it is doubtful if it is really absent in any of the forms known to us. The structural differentiations most usually occurring are the nucleus (Fig. 3, *n*) and the contractile vacuole (Fig. 3, *cv*). The former, as was noticed in the preceding chapter, is of great importance to the cell, and it is questionable whether it is really absent even in those Rhizopods in which it has not yet been discovered. It is presumable, of course, that it is a structure which has gradually become elaborated, that has evolved, and that in the simplest conceivable organism it may have been undifferentiated, but whether such an organism now exists is questionable. The contractile vacuole is excretory in its function, fluid containing products of metabolism in solution accumulating at one or more definite regions of the protoplasm to form it, and being by the sudden and rhythmical contraction of the surrounding protoplasm periodically expelled from the body.

Various degrees of complexity are, however, found among the Rhizopods, the higher forms presenting a considerable degree of differentiation both in structure and in the modes of reproduction, and three orders based upon structural characteristics may be distinguished.

1. Order **Foraminifera.**

The Foraminifera contains the simpler members of the class. In the genus *Amœba* (Fig. 3) are organisms presenting the simple characters above alluded to, being simple naked masses of protoplasm containing a nucleus and a contractile vesicle and presenting a slight differentiation into a peripheral more transparent *ectoplasm* and a central more granular *endoplasm* in which the nucleus is imbedded. The pseudopodia are as a rule blunt lobose processes, though in some species they are more or less filamentous and may even be somewhat permanent. The majority of forms, however, secrete a protective shell of varying composition and complexity. In *Arcella* (Fig. 4) it is chitinous and smooth, and lenticular in shape, completely surrounding the protoplasm, the pseudopodia projecting from the circular opening on the flat surface; in *Euglypha* it is similar in composition, but sculptured on the convex surface; in *Difflugia* the shell is flask-shaped and composed of particles of sand and similar foreign bodies cemented together, while in a large number of forms, especially those which are marine in habitat, the shell is calcareous in composition.

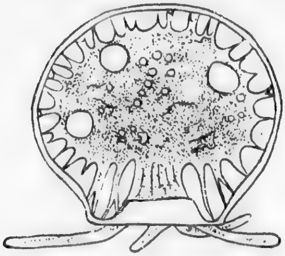

FIG. 4.—*Arcella mitrata* (after LEIDY)

It is in these forms with calcareous shells that the greatest complexity of structure occurs. In some, such as *Gromia*, the shell is simple and flask shaped, the protoplasm protruding from the mouth of the shell and covering its entire surface as a delicate layer, from which the long, slender, and frequently anastomosing pseudopodia take their origin. Although the pseudopodia are practically permanent in form their protoplasm is continually changing, currents streaming from the body towards the tips of the pseudopodia and returning again to the central mass, a constant circulation being thus maintained, and food-particles caught by the delicate pseudopodia conveyed to the central mass, there to be digested. A simple shell is, however, comparatively rare among these calcareous forms; more frequently it consists of several chambers, as in *Miliola*, the chambers varying in size, the first-formed one being the smallest, and, in addition, in very many forms the shell is perforated by minute pores through which the pseudopodia are emitted. The successive chambers are arranged in various ways, sometimes end to end as in *Nodosaria*, sometimes alternately on opposite sides of an axis as in *Textularia*, sometimes as a spiral as in *Globigerina*, sometimes as a helix as in *Rotalia* (Fig. 5), and sometimes more or less irregularly as in *Acervularia*.

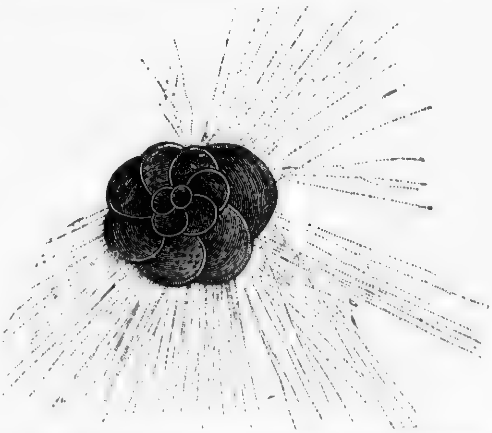

FIG. 5.—*Rotalia venata* (after M. SCHULTZE from HATSCHEK).

Notwithstanding the complexity of the shell, however, the protoplasm retains throughout the order its simple structure, and though in the more complicated forms the single nucleus may be replaced by several, yet beyond this they present no more marked differentiation than is found in the simpler genera.

2. Order **Heliozoa.**

In the second order, the Heliozoa, the pseudopodia are slender as in the calcareous Foraminifera and are permanent and somewhat rigid, the central protoplasm of each one being differentiated into an elastic axial support. The animals are usually globular in shape, the slender pseudopodia radiating out from the central mass, an appearance being thus produced which is sufficient cause for the popular term "sun-animalcule" which is applied to several of the genera, such as *Actinophrys* and *Actinosphærium* (Fig. 6). Currents of protoplasm traverse the pseudopodia as in the Foraminifera and carry the food-particles to the body proper. This has a delicate ectoplasm and a central endoplasm which is frequently highly vacuolated and contains one or more nuclei

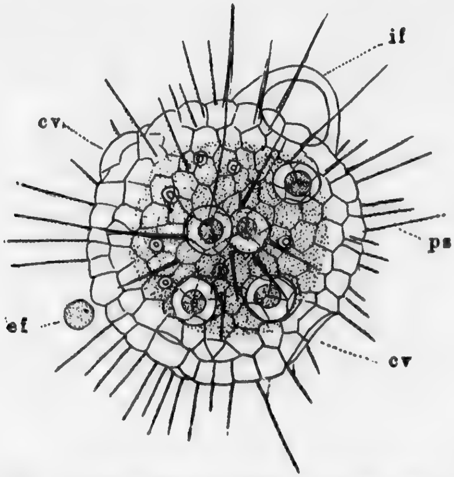

FIG. 6.—*Actinosphærium Eichhornii* (after LEIDY).
cv and *cv'* = contractile vacuoles. *if* = ingested food,
ef = egested food. *ps* = pseudopodium.

and contractile vacuoles. In some forms also a skeleton is developed; it reaches its most perfect form in the stalked *Clathrulina*, in which it consists of a delicate fenestrated siliceous sphere.

3. Order **Radiolaria.**

The Radiolaria are exclusively marine and are the most complicated of all the Rhizopods. Their pseudopodia resemble closely those of the Heliozoa, being slender and possessing an axial support. The body varies in shape somewhat in accordance with the shape of the siliceous shell with which almost all the forms are provided. In those forms in which the shell is simplest, as in *Thalassicolla* (Fig. 7), where it is in reality absent, the body is spherical and is clearly differentiated into two regions, not, however, corresponding to the ectoplasm and endoplasm of other Rhizopods. The centre of the body is occupied by a spherical mass surrounded by a firm chitinous covering and forming the *central capsule.* This contains usually many nuclei as well as vacuoles, oil-globules, and in some cases crystals and pigment-granules. The wall of the capsule is probably comparable to the shell of the Foraminifera, being perforated as in those forms by minute pores through which the intracapsular protoplasm becomes continuous with the extracapsular. This latter portion on this supposition, notwithstanding its greater relative thickness, is equivalent to that portion of the protoplasm of the Foraminifera which is outside the shell and from which the pseudopodia arise. It is usually richly vacuolated and pigmented, but contains no nuclei: the axial supports of the pseudopodia traverse it and take their origin from the inner layers which immediately surround the central capsule and are more homogeneous than the outer portions.

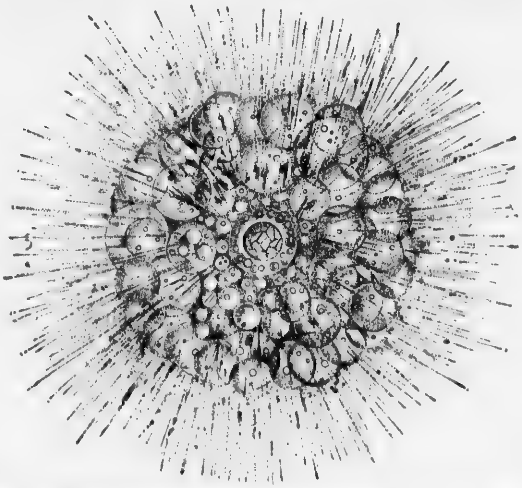

FIG. 7.—*Thalassicolla pelagica* (after HAECKEL from HATSCHEK).

The shell is very various in form in the different genera, reaching a high degree of differentiation in some forms, such as *Heliosphæra* (Fig. 8), where it consists of a fenestrated globe traversed by radiating spines. Its greatest simplicity is seen in *Sphærozoum*, in which it is represented by scattered spicules, while in *Thalassicolla*, already alluded to (Fig. 7), it is entirely absent. As stated, it is usually siliceous in character, though in *Acanthometra* it is composed of a peculiar horny material termed acanthin.

Scattered through the protoplasm of the Radiolarians there are usually to be seen numbers of small yellowish bodies long known as the "yellow cells." They are not constant, however, individuals of any species frequently being destitute of them, a peculiarity due to the "yellow cells" not being really constituent parts of the Radiolarian, but foreign bodies, in fact unicellular plants, for which the term *Zooxanthellæ* has been proposed. They cannot be considered parasites, since they do not appear to exist at the expense of the host, but, on the contrary, their presence seems actually to be beneficial. Mutual benefits are conferred by the plant and the Radiolarian, the coexistence constituting an example of the phenomenon known as *Symbiosis*.

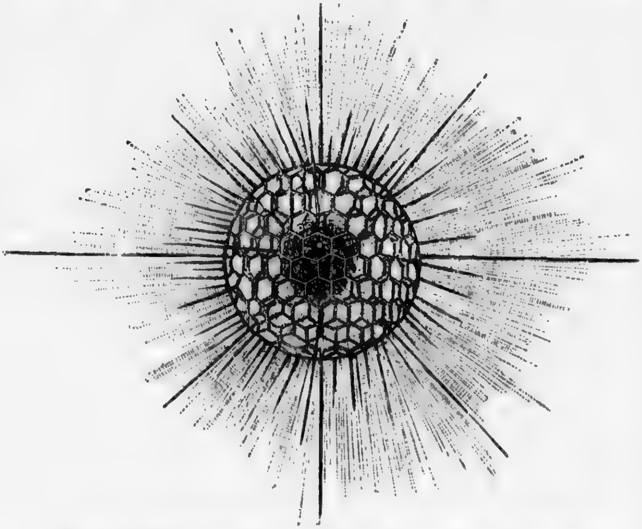

FIG. 8.—*Heliosphæra actinota* (after HAECKEL from HATSCHEK).

Reproduction in the Rhizopods.—Throughout all the groups the simplest form of reproduction, fission, is probably prevalent (Fig. 9), though it is not yet definitely known to occur among the Radiolaria. In the fresh-water Foraminifera and Heliozoa it is, however, the usual method in genera both with and without shells, and it also occurs among the marine Foraminifera. Where the shell is thin it may be divided during the process, but where it is thicker the protoplasm divides within it, one of the individuals retaining the old shell, while the other wanders forth and constructs a new house for itself. This is the case, for instance, in *Arcella*, in which the wandering individual protrudes from the mouth of the parent shell until it forms its new shell, only separating when this is accomplished.

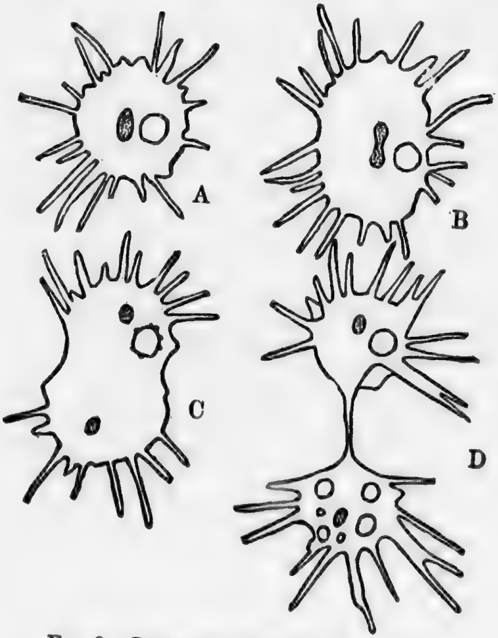

FIG. 9.—Division of *Amœba* (after SCHULZE).

Colonies, produced by repeated divisions and the imperfect separation of the forms so produced, are occasionally formed, but they are simply aggregations of similar individuals, no differentiation or individualization of the colony as a whole occurring. Among the fresh-water Rhizopods this is the case with *Microgromia*, a shelled form, numerous individuals of which may remain in connection with one another by means of their profusely-branching pseudopodia. Colonies of *Actinophrys* are also formed in a similar manner, and among the Radiolaria the forms with rudimentary shells—such as *Sphærozoum*, produce, apparently by the division of the central capsule, numerous individuals which remain in contact.

A modification of fission known as budding or gemmation also occurs in some forms. It differs from fission only in that the products of the division differ in size, so that it is possible to regard the larger individual as the parent and the one or more smaller ones formed from it by budding as the progeny. The process is, however, fundamentally the same as fission and is a derivative of that process. In *Arcella* bud-like processes arise from the periphery of the parent protoplasm, separate, and assume amœboid movement, leaving the shell in an *Amœba*-like condition, and some marine Foraminifera and probably certain Heliozoa reproduce in a similar manner.

Spore-formation also occurs, the parent protoplasm breaking up more or less completely into a number of small portions termed spores, which later increase in size and assume the characters of the parent. This process is sometimes preceded by *encystment*, a phenomenon not, however, in its origin connected with reproduction. It is more prevalent among fresh-water than among marine forms, and seems to have been originally developed as a protection from injurious external conditions, such as the drying up of the pools in which the organisms live. When about to encyst, an *Amœba*, for instance, withdraws its pseudopodia and assumes a spherical shape, and then secretes a more or less dense chitinous case or cyst which completely encloses it. In virtue of the resistent and non-conductive nature of the cyst the organism may, while in this state, suffer uninjured prolonged exposure to conditions which would quickly entail the death of the non-encysted individual, and on the return of favorable conditions may leave the cyst and reassume its active life. Occasionally, too, encystment may occur as the result of good nutrition, an individual which has engulfed a number of diatoms, for instance, secreting a cyst around itself within which it remains until the food-matter has been thoroughly digested, when the cyst is thrown off together with the empty diatom shells and the animal again becomes active.

Plentiful nutrition and reproduction by division (including under this term the various modifications of fission) are related to a certain extent, and it is easy to understand why the two processes of encystment and spore-formation should be associated together. The Heliozoan *Vampyrella* (Fig. 10, *A*) feeds in its active condition on diatoms, and especially on a stalked form, *Gomphonema.* After having digested the contents of the diatom frustules which it engulfs, it pushes them aside and encysts itself upon the stalk previously occupied by them. Within the cyst the animal divides into four spores (Fig. 10, *B*), each of which escaping from the cyst becomes a new *Vampyrella.*

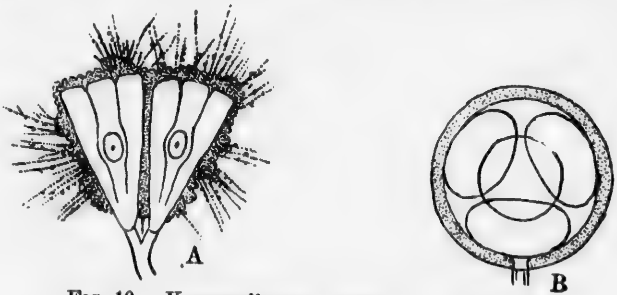

FIG. 10.—*Vampyrella* (from HAECKEL after BÜTSCHLI).

A. *Vampyrella* feeding upon the stalked diatom *Gomphonema.*

B. *Vampyrella* encysted upon the stalk of the diatom.

Among the Radiolaria spore-formation seems to be the most usual method of reproduction, and a complication occurs among them in that spores of two kinds may be formed. In some cases the spores, which are formed from the intracapsular protoplasm, are all equal in size (*isospores*), while in others some of the spores may be large (*macrospores*) and others small (*microspores*). Both macrospores and microspores may be formed in the same individual, or each individual may produce only one of the two forms. In such cases it is easy to determine whether one has to do with macrospores or isospores, which closely resemble each other in size, from the fact that the isospores are spherical in shape and each possesses a peculiar whetstone-like crystal, wanting in the macrospores. All the spores are provided with single whip-like processes, *flagella*, by which they are propelled through the water when set free from the parent.

The various processes so far mentioned concern a single individual only and are therefore non-sexual. Sexual reproduction, consisting of a fusion of two individuals (*conjugation*), seems to be a rather rare occurrence among the Rhizopods, though it has been observed preceding spore-formation in several instances, the fusion being probably the predisposing cause of the spore-formation. In the Foraminiferan *Gromia* the production of spores has been observed, and subsequent conjugation of some of the spores occurs, and it seems exceedingly probable that the macrospores and microspores of the Radiolaria are sexual cells, their further development depending on the conjugation of a micro- with a macrospore, but the fate of these spores has not as yet been ascertained, and their conjugation can only be imagined from analogy with other forms.

II. CLASS **SPOROZOA.**

The Sporozoa, which constitute the second class of Protozoa, are all parasitic, living in the cavities, cells, or tissues of other animals and deriving their nutrition from their hosts. At present much is lacking to an adequate knowledge of various members of the group, but at least three orders are to be recognized.

1. Order **Gregarinida.**

The Gregarinida include some of the largest Sporozoa, and are parasitic either in the body-cavity, intestine, or organs of various Invertebrata (especially in Annelids and Tracheata), or in the cells especially of Vertebrated Animals, these intracellular parasites being usually known as the *Coccidia* in contradistinction to the former, the Gregarinida proper. The members of both groups show a marked differentiation of their protoplasm into ectoplasm and endoplasm, a relatively large nucleus lying in the latter, and none are known to possess pseudopodia. Indeed in many Gregarinida a well-marked cuticle covers the exterior of the body (Fig. 11), sometimes distinctly striated or occasionally tuberculated. The Coccidia and many Gregarinida show little differentiation beyond what has been mentioned, but the Gregarinida which inhabit Tracheate hosts usually present the appearance of being composed of two cells, owing to the anterior portion of the body being separated by a partition of ectoplasm from the posterior part, and in addition to this the anterior moiety in some cases is furnished with hooks, bristles, or finger-like processes (Fig. 11) of use in fixing the animal to the walls of the cavity in which it lives. Even in these cases, however, but a single nucleus is present and the organism is unicellular.

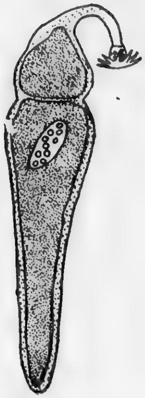
FIG. 11.—*Hoplorhynchus oligacanthus* (after SCHNEIDER).

Reproduction is carried on by spore-formation, preceded in some cases by conjugation (Fig. 12), but simple division or gemmation is not known to occur, apparent instances of division being more probably cases of conjugation. In spore-formation, preceded or not by conjugation, the animal assumes a spherical shape and forms a cyst about itself, the greater portion of the protoplasm splitting up into usually number of nucleated spores, a small portion of it, however, remaining undivided (*residual body*) (Fig. 12). When mature the spores are usually spindle- or boat-shaped and have received the name of *pseudonavicellæ*. They do not, however, develop directly into Gregarines, but their protoplasmic contents break up into 2, 8, or more crescentic spores (Fig. 12), a residual body being again formed as in the formation of pseudonavicellæ. The further history of these crescentic spores is not thoroughly known, but in some cases (*Porospora* from the intestine of the lobster) each seems to become converted into an amœboid structure which later elongates to an actively moving thread-like organism, the *pseudofilaria*, and this, gradually losing its motility, develops into the adult form.

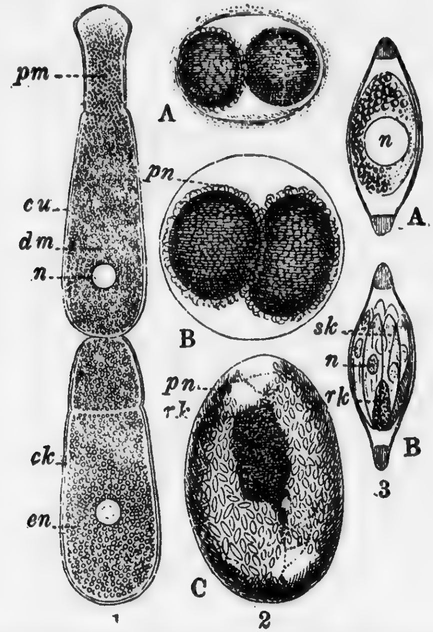

FIG. 12.—REPRODUCTION OF GREGARINE (from HERTWIG).

1. *Clepsidrina blattarum* in conjugation; *ck* = ectosarc, *en* = endosarc, *cu* = cuticula, *pm* = anterior portion, *dm* = posterior portion, *n* = nucleus.
2. Cysts in transformation into pseudonavicellæ; *pn* = pseudonavicellæ; *rk* = residual protoplasm.
3. *A*, a pseudonavicella strongly magnified; *B*, the same divided into spores, *sk*; *n* = nucleus, *rk* = residual protoplasm.

One of the Coccidia, *C. oviforme*, is very common in the liver of rabbits and has also occasionally occurred in Man. It is found encysted in the interior of nodules in the liver, and the development goes no further than encystation in the body of the host. On escaping from the body, however, each *Coccidium* breaks up into four spores, and the contents of each spore later divide into two comet-like bodies (sporozoites) which, when swallowed by a rabbit, make their way to the liver, where they encyst.

2. Order **Myxosporidia.**

The Myxosporidia are found almost exclusively parasitic in Fishes, affecting principally the skin, but also occurring in the internal organs, such as kidneys, spleen, and urinary bladder. They consist of irregularly-shaped masses of protoplasm, sometimes reaching a length 0.1 mm., but usually falling considerably short of this size. Frequently they are enclosed in cysts developed from the tissues of the host, but when not so enclosed seem to possess the power of slow amœboid movement. The endoplasm is usually well differentiated from the ectoplasm and contains in the adult condition a large number of minute nuclei.

Reproduction by division is not known to occur, spore-formation being the only method as yet observed. In the Myxosporidium occurring in the urinary bladder of the Pike the protoplasm breaks up into a number of spherical masses each containing a number of nuclei. The fate of all of these masses is not known, but some, containing only six nuclei, form a wall about themselves and divide into two portions each of which contains three nuclei. These trinucleated bodies elongate, develop a wall, and become pseudonavicella-like spores, one of the three nuclei persisting as the spore-nucleus, while the other two, situated at the extremities of the spore, seem to give rise to a sac-like structure containing within its interior a spirally rolled filament which is emitted when the spore is subjected to pressure and probably serves for the fixation of the spore to the body of a host. The further history of the spores is not thoroughly known, but it seems probable that the contents escape as amœboid masses which develop into adult Myxosporidia.

In many respects the Myxosporidia resemble closely the Gregarinida, but the possibility of their being in reality not of an animal but of a plant nature must not be overlooked. By some authors their nearest relations have been found in the Myxomycetous and Chytridiaceous fungi, a view which certainly has not a little to recommend it.

3. Order **Sarcosporidia**.

The Sarcosporidia are, with a single exception. parasites in the muscle-tissue of warm-blooded animals, especially of Mammalia, being found in the interior of the primitive fibrils of the striated muscles, whose contents they more or less destroy.

They form somewhat elongated sacs 1–2 mm. in length, the wall of the sac being formed of a distinct membrane which has the appearance of being covered with fine bristles. The contents of the sac consist of a protoplasmic ground-substance in which a large number of nuclei are imbedded, sometimes aggregated into masses each of which is surrounded by a delicate membrane. It seems probable that these masses represent a process of spore-formation, but as yet nothing is known regarding the further development of the spores.

4. Order **Hæmosporidia.**

The Hæmosporidia are a group of forms which occur in the blood of various Vertebrates, one of the most interesting of them being the cause of intermittent fever in Man. This form occurs as an amœboid body in the interior of the blood-corpuscles, causing these to enlarge. The growth of the amœboid stage is completed in forty-eight hours, and the organisms then divide into fifteen or twenty spherical "spores" which pass out of the corpuscles into the blood-plasma, entering later new corpuscles. This is the history of the form which produces tertian ague; the quotidian and quartan varieties of the disease are produced by forms requiring respectively twenty-four and seventy-two hours for the completion of their life-cycles.

In association with these *Hæmamœba* forms there also occur sickle-shaped bodies termed *Laverania* whose exact significance is not yet understood, and, furthermore, there is sometimes found free in the blood-plasma a flagellate structure which is probably a degeneration stage of the *Hæmamœba.*

III. CLASS **FLAGELLATA.**

The Flagellates are characterized by the possession of one or more long filamentous processes of protoplasm, known as *flagella,* which, by whip-like movements, propel the organisms through the water in which they live, and at the same time by the production of currents in the water bring food-particles within their reach. Some forms possess pseudopodia in addition to the flagella, which are indeed simply attenuated and mobile pseudopodia, but the majority have a more or less permanent body-form. This in many species is accompanied by the formation at the exterior of the body of a skin or cuticle which in some cases, as in the Dinoflagellata, may assume a sufficient density and thickness to entitle it to be termed a shell.

1. Order **Autoflagellata.**

In the Autoflagellata the body is usually more or less oval, and while in many forms it is naked and capable of changing form (Fig. 13, *A*), yet in others special cuticular investments may be present, taking the form in some cases of a simple cuticular covering, as in *Euglena* (Fig. 13, *B*), in others forming a stalk by which the organism is attached to a foreign body; in some forms, as in *Codosiga* (Fig. 13, *C*), a cuticular collar surrounding the base of the flagellum is present, while in others, such as *Dinobryon*, a cup is formed, within which the organism lives.

Usually but one or two whip-like flagella are present, though occasionally a larger number (6 or 8) may occur, and in some instances one or more may assume a firmer character and serve for fixation of the organism. All forms possess a single nucleous and a contractile vacuole. In the simpler forms, such as *Monas*, in which no cuticle is developed, no special mouth-orifice is present, though the ingestion of food takes place at a more or less definitely localized region at the base of the flagellum, the food-particles drawn to the organism by the currents established by the flagellum usually impinging at this point; where, however, a definite cuticle or shell is developed a definite mouth occurs, and in some cases, as *Euglena* (Fig. 13, *B*), this leads into a

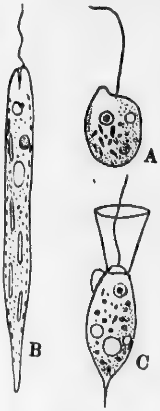

FIG. 13.
A, Oikomonas (after BÜTSCHLI).
B, Euglena acus.
C, Codosiga (after BÜTSCHLI).

distinct tubular pharynx projecting some distance into the interior. No hollow digestive tract is, however, present, but the food-particles, after traversing the gullet, are received directly into the protoplasm of the body, and are digested there as in *Amœba.* A localized egestive region, situated usually towards the posterior end of the body, has been ascertained to occur in some species, but in no instance is it a permanent orifice, as is the case with the mouth. In addition to the nucleus, contractile vacuole, and food-particles, other definitely organized particles. such as starch-like granules and pigment-granules, may by imbedded in the protoplasm. In *Euglena* the pigment is green and resembles plant-chlorophyll, probably too possessing a similar function. A red pigment-spot (stigma) is also present in this and other genera at the base of the flagellum and is supposed to be concerned in light-perception.

The typical Flagellate is a free-swimming single organism, but many forms are fixed, developing a stalk by which they are fastened to foreign bodies; the stalk may be very much branched, each terminal branch supporting an individual, the whole thus forming a colony, without, however, any differentiation among the individuals. Free-swimming colonies also exist, such for example as *Volvox,* in which a large number of individuals are grouped together to form a spherical hollow colony. Each individual contains chlorophyll-granules and a red stigma, and is provided with two flagella by the action of which the entire colony is propelled through the water with a rotary motion.

2. Order **Dinoflagellata.**

The Dinoflagellata are distinguished from the members of the preceding order by the almost general occurrence of a rather dense shell composed of plates of a substance resembling closely vegetable cellulose. Some of the forms, such as *Ceratium* (Fig. 14), present a rather bizzare shape on account of the shell being prolonged into horns, and in the majority the shell-plates are delicately sculptured, while arround the equator of the shell runs a furrow, and from an opening in the line of the furrow two flagella protrude, one of which possesses the ordinary whip-like character, while the other lies in the furrow and in some cases has the form of a delicate undulating band. Chlorophyll-like pigment is almost invariably present, as is also the red stigma. Peculiar cysts are also present in the protoplasm of many forms, consisting of a hollow capsule having rolled up within it a hollow thread, which on occasion may be rapidly evaginated and no doubt has a protective function, resembling very closely in its structure the nematocysts of the Cœlenterates.

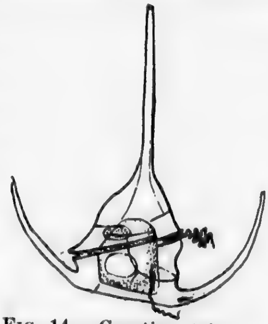

Fig. 14.—*Ceratium tripos* (a combination of two figures by Bütschli).

3. Order **Cystoflagellata.**

The order of the Cystoflagellata includes only two genera, *Noctiluca* and *Leptodiscus*. The latter is a somewhat disk-like structure nearly 2 mm. in diameter, while *Noctiluca* (Fig. 15) is almost globular with a slight depression at one point where the flagella are situated, and at the botton of which is situated the mouth-opening. *Noctiluca* has the form of a cyst, possessing an external thin membrane-like outer wall, to which branching strands of protoplasm extend from the central mass containing the nucleus and lying slightly below the depression which contains the flagella. These are two in number, one being short and whip-like, while the other, usually known as the "tentacle" (Fig. 15, *t*), is a highly contractile, somewhat flattened, and, relatively to the flagellum, thick process of the internal protoplasm. This structure is unrepresented in *Leptodiscus*, which otherwise closely resembles *Noctiluca*.

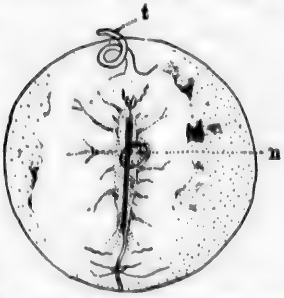

Fig. 15. — *Noctiluca miliaris* (after Bütschli).
t = tentacle. *n* = nucleus.

Noctiluca is of considerable physiological interest, since it is one of the forms to which the phosphorescence of the ocean is due. The cause of the light and its character are, however, as yet unknown.

Reproduction in the Flagellata.—The most frequent method of reproduction in all the orders of the Flagellates is simple division, either transverse or longitudinal. Encystment, followed or not as the case may be by spore-formation, is also common, and when accompanied by spore-formation may be preceded by the conjugation and fusion of two individuals. In *Cercomonas* the spores are exceedingly abundant and small, presenting the appearance of minute granules even under the highest powers of the microscope, but in other forms, as *Chlamydomonas*, the spores are larger and much fewer in number, being only 4 or 8 in this particular case. An interesting modification occurs in closely-related species (Fig. 16), some individuals of which divide into a number of small spores (*microspores*), while others undergo a more restricted division and give rise to a few large spores (*macrospores*). The latter develop directly into the adult forms, but the microspores show a tendency to conjugate in pairs before undergoing further development. This differentiation of two kinds of spores is carried still farther in other forms where neither macro- nor microspores develop directly but further development is contingent upon the conjugation of a micro- with a macrospore.

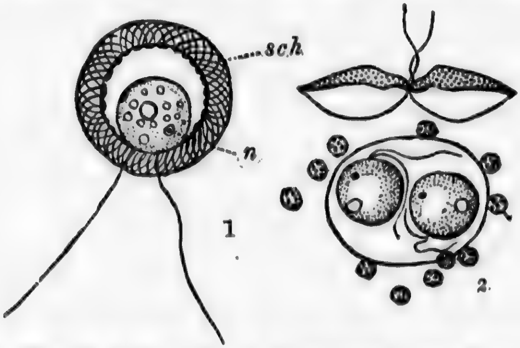

FIG. 16.—1. *Phacotus lenticularis;* 2. MACROSPORES AND MICROSPORES OF THE SAME SPECIES (after BÜTSCHLI).
sch = shell. *n* = nucleus.

In this respect considerable interest attaches to *Volvox*; certain cells, usually those situated in the posterior hemisphere, enlarge and project into the interior cavity, dividing when they have reached their full growth into a number of cells which arrange themselves in a hollow sphere forming daughter colonies in the interior of the parent. In addition to this a sexual process occurs ushered in by certain individuals gradually enlarging, and leaving their position at the surface of the colony. In the interior some of them continue to enlarge, forming *ova* (macrospores), while others divide frequently, forming packets of elongated cells furnished with flagella; these may be termed *spermatozoa* (microspores). The ova develop into colonies similar to the parent after conjugation with spermatozoa. Since many of the cells of the parent colony do not participate in this reproductive act, but disintegrate and die on the development of the daughter colonies, it is clear that we have in this form a rather marked differentiation of the individuals of the colony, the individualities of the constituent cells being to a slight extent merged in the individuality of the colony.

In *Noctiluca* in addition to simple division a process of reproduction occurs which partakes of the character of budding. It is apparently preceded by the conjugation of two individuals, the combined central protoplasms coming to the surface of the cyst where they form a protuberance. Repeated division of the nucleus into 2, 4, 8, etc., up to 256 or more now takes place accompanied by only a partial division of the protoplasm, so that the surface of the protuberance is covered by a large number of bud-like structures. Eventually these separate, develop a flagellum, and take on the character of motile spores. Their further development into the adult *Noctiluca* has, however, not yet been followed.

IV. CLASS **INFUSORIA**.

The Infusoria are the most highly specialized of all the Protozoa, showing a differentiation of the protoplasm unattained by other members of the group. They are characterized by the possession during the whole or part of their lives of numerous delicate short motile hair-like processes termed *cilia* by means of which locomotion is performed and food procured. In one of the orders into which the class may be divided, the Ciliata, these structures are present during the adult life of the organisms, while in the other, the Suctoria, though present in the young stages they are replaced later by immovable processes of the body, which extract the nourishment from the food-particles which come into contact with them.

1. Order **Ciliata.**

The Ciliata are for the most part free-swimming organisms, though some, e.g. *Vorticella* (Fig. 17, *C*), adhere to foreign bodies by means of a stalk, similar to that found in Flagel-

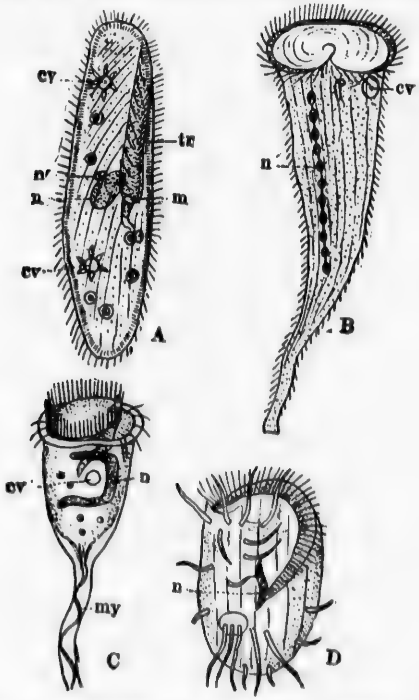

Fig. 17.—A, *Paramœcium*; B, *Stentor*; C, *Vorticella*; D, *Euplotes*.

cv = contractile vacuole.
m = mouth.
my = myophane.
n = nucleus.
n' = micronucleus.
tr = trichocyst.

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lates, and colonial stalked forms also occur as in that class. In these stalked forms the body is enveloped in a chitinous case, of which the stalk is a prolongation, the surface opposite the stalk being, however, left naked and being surrounded by cilia which are absent on the portions of the body protected by the chitin (*Peritrichous* forms, Fig. 17, *C*). In the free-swimming forms, however, the cilia are more universally distributed, covering either the entire surface (*Holotrichous* forms, Fig. 17, *A*) or else one surface of the flattened body, some of them in this case being modified into stout movable bristles upon which the animal creeps (*Hypotrichous* forms, Fig. 17, *D*).

A definitely localized mouth-opening is always present, situated frequently at the extremity of a peristomial groove and leading into a gullet of variable extent, usually lined by cilia, though sometimes furnished with a chitinous support (*Chilodon*). There is, however, no special digestive tract, the food-particles after traversing the gullet being received into the body-protoplasm, where they are digested. Usually there is a localized egestive region, and in a few cases there is a definite anal opening. The food is procured as in the Flagellates by the currents set up in the water by the cilia carrying minute organisms to the neighborhood of the mouth, the cilia surrounding this opening directing them to the gullet.

The body-protoplasm is usually very granular in its central part, and filled with food-vacuoles and products of digestion. Pigment-granules are sometimes present and may consist of Chlorophyll, as in *Stentor*, and one or more excretory contractile vacuoles are always present. The nucleus is usually single, though occasionally two are present, and in the genus *Opalina*, which occurs in the intestine of the Frog, they are numerous in the adult condition. When single the nucleus may be very large and either spherical, elongated, horseshoe-shaped as in *Vorticella* (Fig. 17, *c*), moniliform as in *Stentor* (Fig. 17, *B*), or otherwise shaped. In addition to the nucleus there are one or two minute structures usually to be found in its vicinity which play an important part in reproduction and are known as *micronuclei* (Fig. 17, *A*, *n'*). Other differentiations of the protoplasm are also found in certain forms, as, for instance, special bands differentiated so as to be specially contractile and therefore corresponding in function to the muscles of the higher animals, and hence termed *myophanes.* In *Vorticella* a more striking differentiation of specially contractile protoplasm occurs (Fig. 17, *C, my*); running in an open spiral through the centre of the supporting stalk of this organism is a strong myophane terminating above in the protoplasm of the animal. When the latter is stimulated the myophane contracts, throwing the stalk into a close spiral and withdrawing the animal from the source of irritation. In some of the Holotricha, such as *Paramœcium*, numerous minute rod-like structures occur imbedded in the protoplasm near the surface of the body (Fig. 17, *A, tr*). They are apparently defensive in function, since when stimulated they suddenly, as if by an explosive action, become transformed into long threads or needle-like structures projecting beyond the cilia. These *trichocysts* also occur in some Flagellates.

2. Order **Suctoria.**

The Suctoria lack the active movements of the Ciliata, being destitute in the adult stage of cilia, and many of the forms, e.g. *Acineta* (Fig. 18), are attached to foreign bodies by a stalk. They do not possess any mouth, but a number of simple or branched (*Dendrocometes*) stiff processes project from the body which serve for the prehension of the organisms, principally Amœbæ, upon which they feed. A contractile vacuole and nucleus are always present, the nucleus having sometimes a very complicated shape. It seems pretty clear that they have been derived from the Ciliata, since in their young stages they are free-swimming ciliated structures; the tentacular processes have been compared to the pseudopodia of the Rhizopods, but good reasons for such an homology do not exist, and it is more probable that they are structures peculiar to the group.

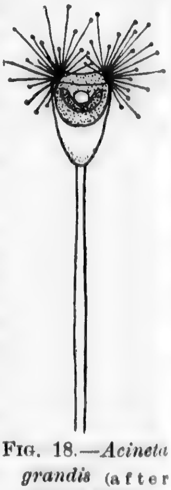
FIG. 18.—*Acineta grandis* (after SAVILLE KENT).

The Reproduction of the Infusoria.—In the Infusoria the reproductive processes reach a much higher grade of complication than occurs in other Protozoa, though the simple processes of fission and spore-formation likewise occur. The former occurs in the majority of forms, and may be the only mode of reproduction occurring throughout a number of generations. Long-continued fission seems, however, to lead in many cases to structural and physiological derangements, unless the process of conjugation be interposed.

Encystment is also of frequent occurrence and may occur under various conditions. In *Colpoda,* in which the process has been most thoroughly studied, encystment may or may not be followed by reproduction. In the latter case the cyst, a resting cyst, is perfectly closed, and the walls are thick and resistent so as to withstand unfavorable conditions, such as insufficient aeration or dryness. When reproduction is associated with encystment it may be either fission or spore-formation. The division cyst is thin-walled and is not completely closed, and within it the animal undergoes division into two or four parts. In spore-formation a thin cyst is first formed, within which the animal slowly rotates, at the same time gradually growing smaller by the expulsion of fluid. Finally it contracts to a round mass and surrounds itself with a second cyst within the first. At the surface of the encysted animal from eight to thirty minute spherical and highly refractive bodies appear which are the spores, and by the bursting of the cyst they, with the remains of the protoplasm in which they arose, escape to the exterior and soon begin to develop. Losing its spherical shape each spore becomes amœboid; then, drawing in all the pseudopodia but one, which elongates and becomes a flagellum, it passes from the Rhizopod to the Flagellate stage; and finally the flagellum is withdrawn, cilia appear, and the animal gradually assumes the adult form. Spore-development somewhat similar to this has been observed also in *Vorticella*, and special interest attaches to it as probably indicating the line of descent of the Infusoria.

Conjugation is a frequent process among the Infusoria, where it seems to have a rejuvenating rather than a strictly reproductive function. If prevented, and fission goes on through a number of generations, marked degeneration ensues; while if it be allowed, the same number of generations may be produced without any signs of degeneration. The process consists of a renewal of the nuclei and micronuclei of the conjugating forms, and the process as it occurs in *Colpidium colpoda* may be described thus. Two individuals come into contact by the anterior portions of their body, actual fusion of the two protoplasms taking place at the point of contact. The micronucleus in each individual then enlarges and divides, the two thus formed subsequently dividing again, so that each of the conjugating individuals contains four micronuclei and one nucleus. One of the four micronuclei in each individual now divides, and one of the two thus formed (the male pronucleus) crosses over to the other individual and unites with the other product of the division, the female pronucleus, there being thus a mutual interchange of micronuclei. The individuals now separate and resume their independent existences, and a rearrangement of the nuclear structures accompanied by fission takes place. The three micronuclei which did not take part in the formation of the pronuclei of conjugation degenerate, as does also the original nucleus. The conjugation micronucleus, formed by the fusion of the male and female pronuclei, divides twice, forming four micronuclei, and this is followed by a fission of the entire Infusorian, each of the daughter forms so produced possessing

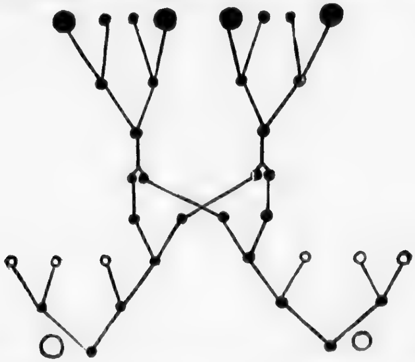

FIG. 19.—DIAGRAM TO ILLUSTRATE THE BEHAVIOR OF THE NUCLEI AND MICRONUCLEI DURING CONJUGATION IN INFUSORIA (after MAUPAS).

two micronuclei. One of these, enlarging, becomes the new nucleus, while the other remains as the micronucleus. This complicated process may perhaps be better followed in the accompanying diagram (Fig. 19).

In the majority of forms the conjugation is a temporary process, the two individuals separating after the exchange of pronuclei. In *Vorticella*, however, a permanent fusion occurs. By repeated longitudinal fission a *Vorticella* becomes divided into a number of small individuals which leave their stalks and swim about freely in the water. Should one of them come into contact with a large individual a complete and permanent fusion of the small with the large one occurs.

SUBKINGDOM PROTOZOA.

I. Class RHIZOPODA.—Protozoa with lobe-like or filamentous pseudopodia.
  1. Order *Foraminifera.*—Pseudopodia without axial support; shell when present horny or calcareous.
    (*a*) Shell absent. *Amœba.*
    (*b*) Shell horny. *Arcella, Euglypha.*
    (*c*) Shell of foreign particles cemented together. *Difflugia.*
    (*d*) Shell calcareous, imperforate. *Gromia.*
    (*e*) Shell calcareous, perforate. *Miliola, Nodosaria, Textularia, Globigerina, Rotula, Acervularia.*
  2. Order *Heliozoa.*—Pseudopodia slender, with axial support; shell if present siliceous; no central capsule.
    (*a*) Shell wanting. *Actinophrys, Actinosphærium, Vampyrella, Microgromia.*
    (*b*) Shell present. *Clathrulina.*
  3. Order *Radiolaria.*—Pseudopodia slender with axial support; shell usually present and siliceous (rarely horny); central capsule present.
    (*a*) Shell wanting. *Thalassicolla, Sphærozoon.*
    (*b*) Shell siliceous. *Actinomma, Heliosphæra.*
    (*c*) Shell horny. *Acanthometra.*

II. Class SPOROZOA.—Parasitic; without pseudopodia, flagella or cilia.
  1. Order *Gregarinida.*—Parasitic in cavities of the body especially of Invertebrates or in the cells especially of Vertebrates.
  2. Order *Myxosporidia.*—Parasitic usually in the skin, sometimes in internal organs of fishes.
  3. Order *Sarcosporidia.*—Parasitic in the muscle-fibres of Mammalia.
  4. Order *Hæmosporidia.*—Parasitic in the blood of Vertebrates.

III. Class FLAGELLATA.—Provided with one or more flagella.
  1. Order *Autoflagellata.*—Without shell, protoplasm not especially vacuolated.

- (*a*) Without collar.—*Monas*, *Cercomonas*, *Chlamydomonas*, *Euglena*, *Volvox*.
- (*b*) With collar.—*Codosiga*, *Dinobryon*.

2. Order *Dinoflagellata.*—With shell composed of cellulose. *Ceratium.*
3. Order *Cystoflagellata.*—Without shell, protoplasm highly vacuolated, marine. *Noctiluca*, *Leptodiscus*.

IV. Class INFUSORIA.—Provided with cilia or immovable processes.

1. Order *Ciliata.*—Provided with cilia in adult stage.
    - (*a*) Cilia of nearly uniform length all over the body (*Holotricha*). *Paramœcium*, *Colpoda*, *Colpidium*, *Chilodon*, *Opalina*.
    - (*b*) Cilia around anterior end of body longer than the rest (*Heterotricha*). *Stentor*.
    - (*c*) Cilia limited to anterior end of body (*Peritricha*). *Vorticella*.
    - (*d*) Cilia or setæ only on ventral surface of the body (*Hypotricha*). *Stylonychia*.
2. Order *Suctoria.*—With cilia only in the young stages, in the adult with immovable processes. *Podophrya*, *Acineta*.

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CHAPTER III.

SUBKINGDOM METAZOA.

THE Metazoa are equivalent to colonies of Protozoa, the individual cells of which have differentiated in various directions, some being more especially contractile, others nutritive, others irritable, others reproductive, etc., instead of each one for itself performing equally all the functions necessary for existence. A *physiological division of labor* of a more or less perfect kind is introduced among the individuals composing the colony, and the welfare of each individual becomes dependent upon the proper performance by its colleagues of their special functions; in short, the individualities of the component cells are merged in the higher individuality of the whole organism.

Physiologically a Metazoon is equivalent to a Protozoon, but morphologically it is the equivalent of a large number of them. Each is physiologically an individual, but morphologically the Metazoon is a colony of Protozoan individuals. To harmonize the physiological and morphological conceptions of an individual it is necessary to recognize several grades of morphological individuality of which the cell may be assumed to be the lowest. In the Metazoa the physiological differentiations of the cell-individuals are accompanied by structural differentiations, so that it is possible, as a rule, to determine from its structure what the function of a cell may be; aggregates of similar cells are termed *tissues* or *tissue-individuals*, and as the simplest Metazoa are complexes of various tissues, such a complex forms the third grade of individuality and may be termed an *Organ-individual*. A complex of organ-individuals united to form a physiological unit constitutes an individual of the third grade, the *Metamere-individual*, while the fourth grade, the *Cormus*, is formed by a similar union of a number of metameres, as, for instance, in the Earthworm, each joint or segment of which is a metamere.

It has been pointed out that the Flagellate *Volvox* presents a tendency towards a higher individuality, being somewhat higher than a mere colony of cell-individuals and yet not quite reaching the dignity of an organ-individual; similarly intermediate conditions between the other grades may occur. In certain worms, for instance, considerable independence of the constituent metameres exists, any one of them, when detached, being capable of carrying on an independent existence, and of developing into an organism similar to that of which it was originally a part. In the Earthworm the dependence of the various segments or metameres upon one another is greater than this, but in it, too, a certain amount of independence is shown by the power it possesses of regenerating lost metameres. In other cormi, as, for instance, in the Lobster, the interdependence of the component metameres proceeds still farther, and a differentiation of the various metameres occurs, a process carried to its greatest extent in the higher Vertebrates. A physiological division of labor among the metameres develops, some of them losing, for instance, their excretory organs, while in others these organs lose their excretory functions and serve as ducts by which the reproductive elements may pass to the exterior. The subordination of the metameres proceeds most rapidly and is most complete at the anterior extremity of the organism, leading to the formation of a head bearing highly developed sense-organs and containing a complex nervous system, which represents originally distinct metamere nervous systems, now fused and destitute of all independence.

Sexual Reproduction in the Metazoa.—In cell-individuals it has been seen that fission is the most frequent and simplest mode of reproduction; in the Metazoa this method and its modification, budding, also occurs, but, as a rule, only in forms of a low grade of individuality or in a transition stage between a lower and a higher grade. In organ-individuals it is of frequent occurrence, the imperfect separation of the individuals so produced leading, in many cases, to the formation of colonies, and in cormi in which the integration of the constituent metameres is but slight it also occurs.

In the Protozoa cell-division naturally entails reproduction, but in organ-individuals reproduction of the constituent cell-individuals is not necessarily connected with the reproduction of the entire individual, but may simply increase the number of lower-grade individuals of which it is composed. Similarly multiplication of the organ-individuals of a metamere, or of the metamere-individuals of a cormus may occur without producing reproduction of the whole; it is simply growth. From growth to reproduction by budding the path is short, and various intermediate stages connecting the two processes can be found. Hence reproduction has been aptly defined as "discontinuous growth," though perhaps it would be even more apt to define growth as *reproduction without discontinuity*, growth in a Metazoon depending on the reproduction of the lower-grade individuals of which it is composed.

It is possible to carry this idea still farther back and refer the growth of a cell to the reproduction of the constituent elements, plasomes, of which, it may be imagined, it is composed. In the simplest cells the various forms of plasomes are distributed throughout the cell, but in the higher Protozoa, for instance, an aggregation of similar plasomes occurs, giving rise to such structures as the myophanes. In a similar manner in the lower Metazoa, although a division of labor and structural differentiation has taken place among the constituent cells, yet the cells possessing similar functions, as, for instance, the nerve-cells, are more or less irregularly scattered throughout the body, only becoming aggregated in the higher forms into distinct tissues, and giving rise to the most perfect type of an organ-individual. Likewise in a metamere-individual a multiplication of the organs leads to a transition form with discretely arranged parts, the definite aggregation of which produces a cormus, composed in the simpler forms of distinct metameres, which become more and more integrated and subordinated to the individuality of the cormus in higher types of that grade of individual.

According to this view the segmentation or metamerism of the higher Metazoa is the result of the multiplication and subsequent integration of the organ-individuals of an ancestral metamere-individual, and explains the occurrence of imperfect metamerism in certain forms of that grade of individuality (*Turbellaria*). Some authors have considered metamerism to have arisen by the reproduction by budding of an ancestral metamere, an idea which fails to explain satisfactorily the condition just referred to. The view presented here considers metamerism to be the result of growth. It has not arisen by the reproduction of the metamere, but by that of its organs, just as a typical organ-individual has arisen by the reproduction and integration of its constituent cell-individuals.

As a mode of reproduction in the Metazoa division plays but a secondary part, the sexual process being the characteristic method. Attention has already been called to the partial specialization in *Volvox* of reproductive cells which serve to perpetuate the species, the remaining cells of the colony perishing. This condition is a premonition of the more perfect specialization found in the Metazoa of reproductive or *germ* cells and non-reproductive or *somatic* cells, the latter serving for the nutrition and protection of the germ-cells, to which the perpetuation of the species is entrusted. Comparatively early in the development of an individual certain cells differentiate from the others, not undergoing like them a physiological and structural specialization, but retaining a generalized character. These are the germ-cells usually grouped together to form the reproductive organs.

In describing the methods of reproduction occurring in the Flagellata, the manner of the development of sexual reproduction was indicated. It appears to have been originally a more or less accidental fusion of two similar cells or spores, and from being accidental this fusion gradually became the rule on account of the greater vitality which the conjugate individual possessed over cells which did not conjugate. The next step was the differentiation of microspores and macrospores, which reaches a high development in *Volvox*, where it is associated also with a differentiation into somatic and germ cells. In the Metazoa both these differentiations are carried to a higher degree, the macrospores being known as *ova* and the microspores as *spermatozoa*, while the aggregates of these cells are termed respectively *ovaries* and *testes*.

In a young embryo a mass of germ-cells which is to give rise to spermatozoa cannot be distinguished from one which is destined to be converted into ova. Fundamentally both are the same, and occasionally a portion of a mass of germ-cells may be differentiated into ova, while the rest of it develops into spermatozoa. This has not unfrequently been seen in fishes in which there is normally a separation of the sexual elements in distinct individuals, and throws considerable light upon the occurrence of forms which normally possess both elements. This condition of *hermaphroditism*, which occurs in many parasitic forms and in certain sponges, Flatworms, Mollusks, and Crustacea, seems to have been secondarily acquired. It is probable that the ancestral Metazoa were unisexual, possessing reproductive elements of only one kind, a supposition borne out by the frequent association of hermaphroditism with a parasitic or sessile mode of life, such conditions being what may be termed abnormal, and usually accompanied by marked structural characters which are to be regarded as secondary modifications. On the other hand, it is noticeable that the lowest free Metazoa (such as the free-swimming Cnidaria) are unisexual.

An ovum is a single cell, and in its typical form consists of a mass of protoplasm containing a nucleus, and may or may not be surrounded by a membrane. Seldom, however, does such a simple ovum occur; usually more or less yolk, consisting of fatty and albuminous globules, is distributed throughout the protoplasm, and frequently the amount of yolk far overbalances the amount of protoplasm. Other structures, such as albumen and one or more enveloping membranes, may be added, the ova of different species differing greatly in this respect. Among the lower forms the ova are usually extruded freely from the body of the parent, but in many of the higher Metazoa they are enclosed within protective cases (cocoons), as in the Earthworm, or imbedded in jelly-like masses, as in the common Pond-snails.

In the ovary of a young individual all the germ-cells are alike, and all are potentially reproductive cells; very frequently, however, many of the primitive germ-cells relinquish their reproductive function and serve as purveyors of nutrition to certain of their comrades which enlarge and become mature ova. This is well seen in insects, in which each ovary (Fig. 20) consists of a number of tubes tapering to a point at one end, while at the other they open into a common duct,

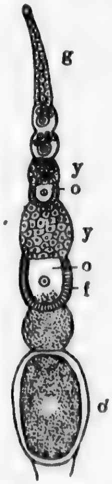


FIG. 20.—OVARIAL TUBE OF A BEETLE (after LUBBOCK).

g = germinal region.
o = ova.
o' = mature ovum.
y = yolk-cells.
f = follicle-cells.

the oviduct, leading to the exterior. At the tip of each tube the primitive germ-cells (Fig. 20, *g*) are located, and lower down ova (*o*) in various stages of development towards maturity are to be found, each surrounded by a number of small undeveloped germ-cells, known as *follicle-cells* (*f*), whose function it is to transfer food-yolk (*y*) to the growing ovum. As the latter approaches maturity the follicle-cells secrete around it a thick, sometimes highly sculptured shell and finally degenerate.

As a rule, conjugation with a spermatozoon, i.e. fertilization, is necessary as an antecedent to further development. Before this takes place, however, certain modifications of the ovum are necessary, the phenomena which accompany them being known as the *maturation of the ovum*. In this process (Fig. 21, *A*) the nucleus approaches the surface of the ovum and there undergoes a karyokinetic division which is peculiar in that in the equatorial-plate stage twice as many chromosomes are formed as are typical for the species. These do not undergo longitudinal division, and by the karyokinesis their number is reduced to the typical number, a small cell, the *polar globule* (*pg*), being separated from the ovum with half the chromosomes, while the others are retained within the ovum. The nucleus of the ovum, instead of now returning to the resting stage, divides again (Fig. 21, *B*), a second polar globule being formed and receiving half the chromosomes

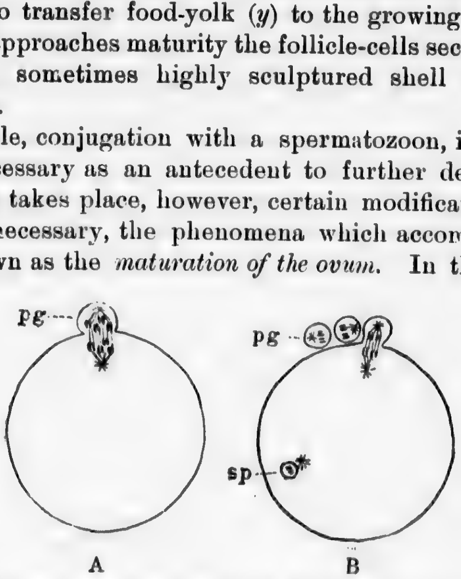


FIG. 21.—DIAGRAMS ILLUSTRATING THE MATURATION OF THE OVUM.

A = formation of the first polar globule (*pg*).
B = formation of the second polar globule and entrance of the sperm-nucleus (*sp*).

which remain, so that the nucleus of the ovum now possesses only *half* the number of chromosomes which are characteristic for the species. At the time of the formation of the second polar globule the first frequently divides without its nucleus passing into a resting stage, so that as the result of this maturation process four cells have been formed, three of which are small, while the third is relatively very large and will alone undergo further development. When these divisions have been completed and the chromosomes have been reduced to one-half their proper number the nucleus of the ovum passes into the resting stage, migrates back towards the centre of the ovum, and is ready for conjugation with the nucleus of a spermatozoon.

The spermatozoa are always much smaller than the ova, and are, as a rule, capable of active motion, though in certain Crustacea, for instance, they lack this power. The ova and spermatozoa have specialized in opposite directions in this respect. The ova of the Metazoa are specialized as the nutritive cells of conjugation, possessing abundant protoplasm and usually a considerable amount of yolk for the nutrition of the young embryo. They consequently have lost their motility, and in order that conjugation may be made probable the spermatozoa lack all unnecessary material which would interfere with their motility, no yolk being stored up and the protoplasm even being reduced to the smallest amount consistent with the development of a locomotor organ. The nuclei, as will be seen later, are essential elements in conjugation, and the spermatozoa are to all intents locomotor nuclei, the ova supplying the protoplasmic nidus necessary for the growth and division of the nucleus formed by conjugation.

In their typical form spermatozoa are composed of a globular or pyriform head consisting of a nucleus surrounded by a small amount of protoplasm, and a long filamentous tail continuous with the protoplasm and frequently provided with a delicate fringe-like membrane (Fig. 22, *F*). By the rapid whipping movements of the tail the organism is propelled through the water, or other fluid in which it may find itself, and so may come into contact with an ovum.

The transformation of the germ-cells present in an embryo into spermatozoa is usually a somewhat complicated process. In the Round-worm *Ascaris*, in which it retains somewhat primitive characters, the process closely resembles what takes place during the maturation of the ovum.

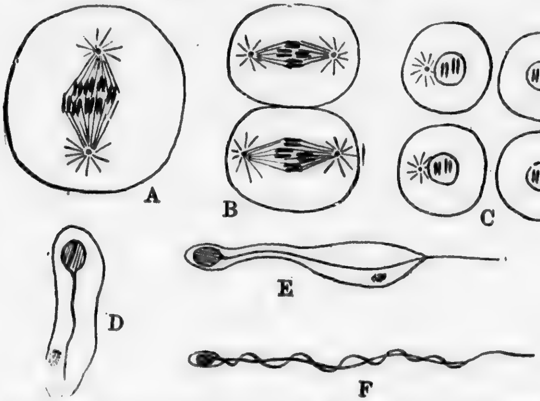


FIG. 22.—DIAGRAMS TO ILLUSTRATE THE MATURATION OF THE SPERM-CELL.

A = division of the spermogone.
B = division of the two spermocytes.
C = the four spermatids.
D, *E* = conversion of a spermatid into a spermatozoon.
F = fully developed spermatozoon.

The embryonic germ-cells (*spermatogones*, Fig. 22, *A*) undergo karyokinetic division, the number of chromosomes being, as in the ovum in the division which results in the formation of the first polar globule, twice that which is characteristic for the species. They do not undergo longitudinal division, and one half of them passes into one of the daughter cells (*spermatocytes*) and the other half into the other, so that these two cells possess the number of chromosomes characteristic for the species. A division of these daughter cells (Fig. 22, *B*) immediately takes place without a return to the resting stage, and unaccompanied by a longitudinal division of the chromosomes, so that four cells (*spermatids*, Fig. 22, *C*) are formed, each of which contains only half the typical number of chromosomes, and each one of these cells becomes a spermatozoon. This process is comparable step by step with the maturation of the ovum and seems to indicate that the polar globules are to be regarded as abortive ova.

The conversion of the spermatids into spermatozoa is simply a differentiation of structures already present. In the air-breathing Mollusca, for instance, the spermatids consist of a mass of cytoplasm containing a nucleus, in close proximity to which may be found the centrosome, while an irregular mass of filaments represents the remains of the spindle-filaments. In the differentiation which follows (Fig. 22, *D*, *E*, and *F*) the nucleus elongates and its chromatin-filaments fuse to form a homogeneous mass; the cytoplasm likewise elongates, and in it appears an axial filament which later will form the tail-filament. The origin of this filament is doubtful, some authors maintaining that it is a differentiation of the cytoplasm, while others believe it to be a prolongation of the nuclear substance; but, however that may be, the spiral fringe which surrounds the axial filament is certainly the remains of the cytoplasm of the spermatid. The remains of the spindle-filaments disappear, while the centrosome probably persists as a structure lying behind the head and termed the "Mittelstück."

In some cases, as the insect *Pyrrhocoris* and the crustacean *Diaptomus*, the doubling of the chromosomes previous to division into spermatocytes does not take place. In *Pyrrhocoris* twenty-four chromosomes are typically present and twelve of these pass into each of the spermatocytes, and in the division of these to form the spermatids each of the twelve chromosomes divides so that each spermatid possesses half the typical number. In *Diaptomus* the same result is brought about somewhat differently. The spermatogones possess eight chromosomes which assume a dumbbell shape and divide transversely, so that each spermatocyte has the typical number of chromosomes; the spermatocytes divide without passing through a resting stage, and each spermatid thus contains four chromosomes, i.e. half the typical number.

Fertilization of the Ovum.—So soon as the formation of the polar globules has been completed, the nucleus of the ovum migrates towards the centre of the protoplasm and is the *female pronucleus* (Fig. 23, *fp*) of conjugation. The penetration of the spermatozoon may occur at any portion of the surface of the ovum and may take place before, during (Fig. 21, *B*, *sp*), or after the formation of the polar globules, a single spermatozoon, as a rule, in healthy ova, penetrating and taking part in the conjugation, though apparently in some cases *polyspermy*, or the penetration of several spermatozoa, may occur. The head of the spermatozoon comes into contact with the protoplasm of the ovum, which in some cases rises up to meet it, and is rapidly engulfed. The tail likewise of the spermatozoon is taken into the ovum and seems to be completely absorbed, the head alone being visible in later stages; it constitutes the *male pronucleus* (Fig. 23, *mp*), and moves towards the centre of the egg until it comes into contact with the female pronucleus, fusing with it to form the *segmentation nucleus*. A spindle now makes its appearance, and the segmentation nucleus passes through the various karyokinetic stages, forming an equatorial plate with the typical number

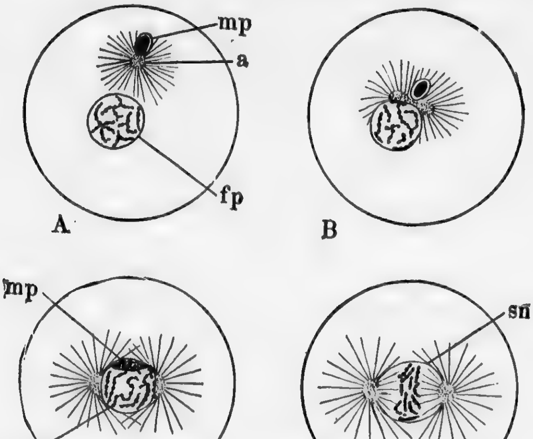


Fig. 23.—Diagrams to Illustrate the Phenomena of Fertilization.
(From figures by E. B. Wilson.)

A, the approximation of the male and female pronuclei.
B, division of the archoplasm.
C, separation of the archoplasm spheres.
D, fusion of the pronuclei, and formation of the segmentation spindle.
fp = female pronucleus.
a = archoplasm.
mp = male pronucleus.
sn = segmentation nucleus.

of chromosomes, which divide longitudinally in the usual manner, one half of them passing towards each of the archoplasm spheres. The ovum then divides into two cells, the nuclei of which each possess chromatin elements from both the male and the female pronuclei.

It will be seen from this that the conjugation or fertilization process consists of the union of two distinct nuclei, whose complete fusion however does not necessarily occur until after the first division or segmentation of the ovum.

The archoplasm of the segmentation nucleus is derived, as a rule, from the sperm-cell alone (Fig. 24), that which existed in the ovum during its maturation disappearing before fertilization takes place. It has been claimed, however, that in some cases the ovum archoplasm persists, and unites with that from the sperm when the pronuclei unite, and that more rarely the ovum archoplasm alone persists. These observations, however, need confirmation.

Furthermore, in some cases at least, it is possible to distinguish the nuclear elements derived from the male and female pronuclei respectively in stages later than the first segmentation, owing to a slightly different behavior to certain staining reagents which characterizes them. The pronuclei undergo a morphological fusion during the first cleavage of the ovum, but a physiological differentiation persists.

Segmentation and Early Development of the Ovum.—The development of the ovum into the embryo consists in its division into a number of cells, which gradually undergo a physiological and morphological differentiation resulting in the formation of tissues, organs, etc. These divisions constitute the segmentation of the ovum.

The first division has already been described; it bears a definite relation to the formation of the polar globules, the plane of the division passing through the point at which they were separated from the ovum. Considering this point to represent one pole of the ovum, the first division is meridional, and the second division likewise, though its plane is at right angles to that of the first division (Fig. 24, *A*). The third division is, on the other hand, equatorial, its plane cutting the planes of previous divisions at right angles (Fig. 24, *B*).

Eight segmentation-cells are thus formed which remain in contact with each other and enclose a small cavity, the segmentation-cavity or *blastocœl*. The further division of the cells (Fig. 24, *C*) results in the formation of an oval or spherical organism (Fig. 24, *D*) which may be compared to *Volvox*, consisting of a single layer of cells enclosing a more or less voluminous blastocœl. This embryonic stage is known as the *blastula*. In its simplest form it shows no special differentiation into tissues, its cells being uniformly ciliated, and the organism free-swimming, moving through the water with a rotatory movement about a definite axis, one and the same end of which is always anterior. In many blastulas, however, especially in those which for one reason or another are not free-swimming, an early differentiation of the cells takes place, especially at the extremity which is posterior in the free-swimming forms or which corresponds to that pole in the non-motile embryos. These posterior cells are usually somewhat larger than those at the anterior pole, and if much food-yolk is present in the embryo it is especially concentrated in

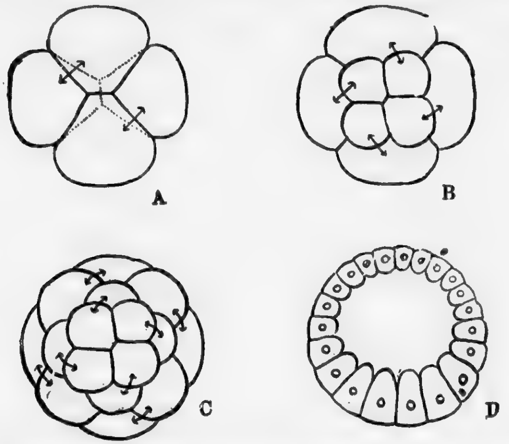


Fig. 24 —Diagrams illustrating the Segmentation of the Ovum.

A, four-celled stage.
B, eight-celled stage of a telolecithal ovum.
C, sixteen-celled stage.
D, blastula.
The arrows indicate the mode of division.

these cells, which in the later development will assume the vegetative functions of the organism.

In many ova the processes just described are modified to a greater or less extent, but from the frequency of their occurrence they must be regarded as fundamental and the modifications as secondary.

Ova which contain but little yolk usually follow more or less closely the typical processes, but where the yolk is abundant, being an inert substance, it acts as a drag upon the protoplasmic activity and produces modification of the segmentation-processes. Two methods of arrangement of the yolk may be recognized: (*a*) it may be aggregated more or less completely at one pole of the ovum, such ova being termed *telolecithal*, or (*b*) it may be distributed in the meshes of a protoplasmic network, a small quantity of yolkless protoplasm being concentrated around the nucleus of the ovum, while another portion of it forms a thin peripheral layer surrounding the yolk, this arrangement being termed *centrolecithal*.

In telolecithal ova the third segmentation-division results in the formation of four cells containing very little yolk at one pole of the ovum, while nearly all the yolk is concentrated in the four cells at the other pole (Fig. 24, *B*). This arrangement, which occurs in many Mollusca, constitutes what is termed a *total irregular* segmentation, in which, owing to the large size of the yolk-containing vegetative cells, the blastocœl is usually comparatively small. In the Squids the amount of yolk present at the vegetative pole is very great and the protoplasm of the ovum collects upon its surface, there undergoing division and producing a plate of cells, the blastoderm, which by further division gradually extends and finally encloses the inert yolk. This *partial* segmentation is the result of the presence of a very large quantity of yolk and its telolecithal arrangement, and necessarily obscures greatly the blastula stage.

In centrolecithal ova which occur in Crustacea and Insects, the division of the nucleus is accompanied by a division of the central yolkless protoplasm only, the yolk-containing reticulum and the peripheral layer not taking part in the process. As the divisions continue the nuclei gradually approach the surface and finally come to lie in the peripheral protoplasm, which then takes part in the division, a greater or less portion of the inert undivided yolk occupying the blastocœl of the resulting blastula. Many intermediate gradations occur between such a typical centrolecithal and a total regular segmentation, from which both the centrolecithal and telolecithal methods are to be derived.

The blastula is a single layer of cells surrounding a large blastocœl in typical cases, and is a stage quickly passed over in the Metazoa. It is succeeded by a stage in which the embryo consists of a double-walled sac open at one end, the *gastrula* (Fig. 25). This is most frequently produced from the blastula by the pushing in or *invagination* of the cells of one pole (the posterior in free-swimming blastulas) into the blastocœl, which thus becomes more or less perfectly obliterated. The cavity lined by the invaginated cells is the primitive digestive tract or *archenteron*, its opening to the exterior being the gastrula mouth or *blastopore*. The gastrula is a two-layered organism or is *diploblastic*, and the cell-layers of which it is composed are the *primitive germ-layers*. The outer layer in the higher Metazoa gives rise to the integument, nervous system, and sense-organs of the adult and is known as the *ectoderm*, while the inner one, from which the digestive tract and its glands, such as the liver, will develop, is termed the *endoderm*.

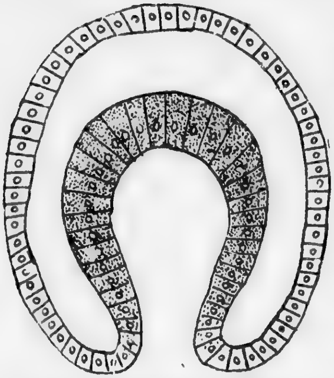


FIG. 25.—DIAGRAM OF A GASTRULA.

Just as the presence of yolk in the ovum may modify the segmentation, so too it may produce decided modifications in the formation of the gastrula. The method just described, which occurs in embryos containing little food-yolk, is distinguished as *embolic* from the *epibolic* method occurring in telolecithal ova which undergo a markedly irregular segmentation. In such ova, as has been stated, one pole is occupied by inert yolk-laden spherules, while at the other are almost yolkless active cells. These latter divide rapidly and extend as a cap over the yolk-laden cells and finally completely enclose them. The result is practically the same as in the embolic method, the yolk-laden endoderm cells being enclosed within the yolkless ectoderm.

Among the lower Metazoa especially, another method occurs by which the diploblastic embryo is formed. Instead of certain cells invaginating, each cell of the blastula divides in a plane parallel to the surface of the organism, one of the two cells thus produced becoming ectoderm, while the other is a portion of the endoderm. A diploblastic closed sac thus results, the blastopore appearing later and placing the archenteron, which in this case is identical with the blastocœl, in communication with the exterior. This process is known as *delamination* (Fig. 26, *A*).

A third method also exists, occurring like delamination in its most typical form among the lower Metazoa. This is the *immigration* method (Fig. 26, *B*), certain cells of the blastula leaving their position at the surface and passing into the blastocœl. Here they undergo division, and, by the addition of other cells by immigration, the blastocœl gradually becomes filled up and a solid organism, consisting of an external layer of cells surrounding a central more or less solid mass, results. This is known as the *parenchymella* or *sterrula.* Later a cavity appears in the centre of the solid mass, whose cells gradually are pushed towards the periphery, where they form eventually a single layer, the *endoderm.* Finally a blastopore is formed and the embryo becomes a gastrula.

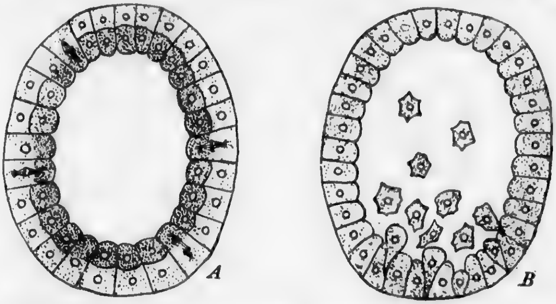


FIG. 26.—DIAGRAM ILLUSTRATING THE FORMATION OF THE DIPLOBLASTIC STAGE (*A*) BY DELAMINATION, (*B*) BY IMMIGRATION.

It does not seem easy to bring the delamination and invagination methods of gastrulation into direct relation with each other, or to derive one from the other, but it is probable that both must be referred back to the immigration method. In typical cases of immigration the cells which migrate are situated irregularly at any part of the blastula, but frequently, especially in free-swimming blastulas, the migrating cells are all located at the posterior extremity. If in such cases of polar immigration the migrating cells were to pass into the blastocœl *en masse* instead of individually, invagination would result. On the other hand, if a considerable amount of yolk were present in all the cells of a blastula, it might happen that, instead of migrating, the cell might undergo division, cutting off the yolk-containing protoplasm from the yolkless, delamination thus taking place.

The fact that in some cases both immigration and delamination may occur simultaneously, leading to the formation of a sterrula, bears out the idea that the latter process has arisen from the former.

Furthermore, it may be pointed out that the occurrence of immigration in such colonial Flagellates as *Volvox* indicates the primitive character of immigration in the Metazoan blastulas, as well as the manner in which diploblastic organisms have arisen from the more primitive single-layered organisms.

It is only in the lowest Metazoa, however, that the adult organism is diploblastic. In all others a *triploblastic* (Fig. 27) condition supervenes during embryonic life, by the development of a third layer, primitively separated from the endoderm, and occupying the space which may remain between the two primitive layers. This is the secondary germ-layer or *mesoderm*. From it there arise the muscular, excretory, circulatory, and reproductive systems in the triploblastic animals, the first and last of these being derived in diploblastic forms from either one or both of the primary layers, while the excretory and circulatory systems are not differentiated.

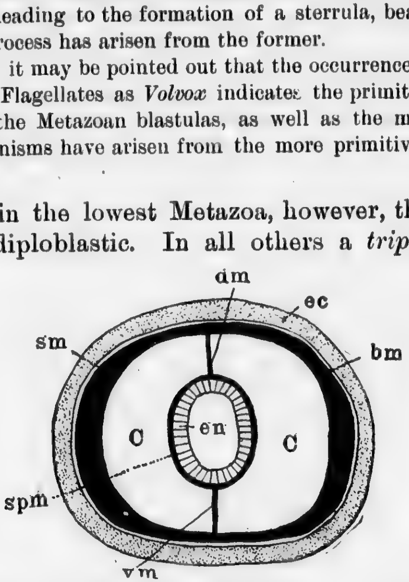


FIG. 27.—DIAGRAMMATIC TRANSVERSE SECTION OF AN EARTHWORM TO SHOW THE TRIPLOBLASTIC CONDITION.

bm = basement membrane.
C = cœlom.
dm = dorsal mesentery.
ec = ectoderm.
en = endoderm.
sm = somatic mesoderm.
spm = splanchnic mesoderm.
vm = ventral mesentery.

The manner of formation of the mesoderm in the embryo varies greatly. In some cases it arises as bilateral pouch-like outgrowths of the archenteron, which later form closed sacks completely surrounding the digestive tract, the sack of either side coming into contact above and below, the united walls forming the dorsal and ventral *mesenteries* which suspend the intestine (Fig. 27, *am* and *bm*). That wall of each sack which surrounds the digestive tract is termed the *splanchnic layer* of the mesoderm (Fig. 27, *spm*), while that lying immediately below the ectoderm is the *somatic layer* (*sm*), and the enclosed cavity is the *cœlom* (*C*) or body-cavity. In other cases the protoplasm destined to give rise to the mesoderm segregates into a small number of cells, or sometimes even into a single cell, at an early period of the development, frequently while the embryo is still in what may be considered the blastula stage. These cells, known as *mesoblasts*, give rise by repeated division in one direction, and by the subsequent division of the daughter cells so formed, to bands of mesodermic tissue extending along the ventral surface of the embryo (see Fig. 105), and later growing dorsally so as to enclose the digestive tract. The cœlom forms by the hollowing out of the mesodermic bands, and when fully developed presents the same appearance as in the former case.

In many animals, such as some Turbellarian worms, a well-developed cœlom is not present, the only traces of it being minute scattered cavities in a mass of mesodermic tissue which fills up the space between the endoderm and ectoderm. A strict demarcation of this form of cœlom (*schizocœl*) from the other variety (*enterocœl*) does not, however, exist, gradations occurring in various groups of animals and both varieties sometimes being coexistent in the same form, as for instance in bivalve Mollusca, where the pericardial cavity is to be regarded as an enterocœl, while the spaces existing elsewhere in the mesoderm are schizocœls.

If the conditions which exist in the lowest triploblastic animals known to us, the Turbellarian worms, throw any light upon the origin of the mesoderm, it would seem that primitively it was a solid tissue, not completely marked off from the endoderm, and that any cœlom that it contained was of the nature of a schizocœl. From this condition it became more and more differentiated from the endoderm proper, and either tended to appear as a separate germ-layer at an early stage of development in the form of the mesoblasts, or was delayed in its development until after the formation of the primitive digestive tract, from which it then separated in the mesodermic pouches. According to this view the mesoderm is a secondary derivative of the endoderm, and the endoderm of the diploblastic organisms is equivalent to the endoderm *plus* mesoderm of the triploblastic forms. The apparent derivation of the mesoderm from the ectoderm in some of the latter (e.g. *Annelida*) is to be regarded as resulting from the precocious segregation of the mesoderm at an early period of development and is not to be regarded as indicating its original derivation.

Non-sexual Reproduction in the Metazoa.—Reproduction by division and by budding, though playing by no means so important a part as in the Protozoa, is nevertheless of frequent occurrence in the Metazoa, especially in certain groups. In certain Turbellarian worms (*Microstoma*) division is the usual mode of reproduction, replacing almost completely the sexual method, and, the individuals so produced remaining in connection with one another, longitudinal chains are produced, consisting of individuals in various degrees of separation (Fig. 28). In certain Annelids also (Naididæ) division frequently takes place, occasionally each metamere being capable of developing into a new animal, as in *Ctenodrilus*.

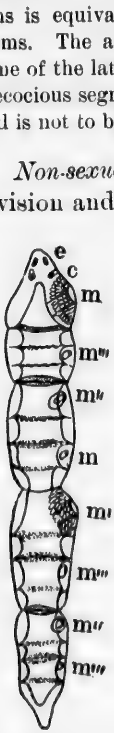


FIG. 28. — DIAGRAM SHOWING NON-SEXUAL REPRODUCTION OF A TURBELLARIAN WORM *Microstoma* (after VON GRAFF).

Budding, however, is a rather more frequent method and is characteristic of certain groups, such as the Hydroids, Anthozoa, and Bryozoa. In some cases, as in *Hydra* and some medusæ, the buds separate from the parent and lead an independent existence; but frequently the separation is not complete, resulting in the formation of colonies the individual components of which are in organic connection with each other. In such colonies a physiological division of labor among the constituent individuals may take place, as in the Hydroid *Hydractinia* (see p. 87) where some of the individuals devote themselves to the nutrition of the colony, others to its reproduction, and others again to the protection of their weaker companions. The assemblages produced by budding may assume very complicated shapes, though occasionally linear colonies are formed which are with difficulty to be distinguished from those formed by division. Indeed a definite distinction between budding and division is not possible, though where an alternation of older and younger individuals occurs in a linear colony division is indicated, while in one produced by budding there is a regular succession of gradually older individuals from before backwards.

Closely related to budding is the power of regeneration of parts. The higher Crustacea possess an extraordinary power of regenerating lost limbs, and provision is present in crabs and the lobster for the self-amputation of a limb when such a mutilation seems to be demanded by the exigencies of the situation. In the lower forms, however, the extent to which such regeneration may be carried is much greater, extending even to the reproduction of the whole by a comparatively small part. A Starfish is not only able to regenerate an arm which has been accidentally lost, but from an arm and a portion of the disk all the missing parts may be developed; and *Hydra* or a Sponge may be divided into a large number of pieces each of which is capable of developing into an entire animal. Such phenomena, as well as budding and division, depend either upon a low degree of differentiation of the tissues, as in such a form as a Sponge or in *Hydra*, or else to the persistence of a certain amount of tissue in an embryonic or undifferentiated condition. In a Bryozoan bud, for instance, as its tissues gradually differentiate into the adult condition, a number of cells lag behind and do not take part in the differentiation, and later give rise to a new bud; and similarly in the Annelid worms the tissues of a regenerating part show an appearance and mode of differentiation similar to what they present in the development from the ovum. Conversely, the greater the degree of differentiation and integration of the tissues and organs of an animal the less is the power of regenerating lost parts or of reproducing by budding.

As a general rule ova are incapable of developing into the adult form unless fertilized by a spermatozoon. In a number of forms, however, a development of unfertilized ova occurs constituting a mode of reproduction known as *partheno-*

genesis. Examples of this phenomenon are to be met with in Insects, a familiar one being the common Hive Bee, the queens of which species deposit large numbers of eggs, those last deposited, which give rise to drones, being unfertilized and developing parthenogenetically. In certain flies (*Cecidomyia*) this parthenogenetic development of the ova may occur while the insect is still in the larval or maggot stage, a phenomenon which is known as *pœdogenesis* (Fig. 29).

Alternation of Generations.—The majority of forms which possess the power of non-sexual reproduction also reproduce by the sexual method, no definite relation existing, however, between the two processes. In some cases, however, a definite relation is established, the one method succeeding the other with rhythmic regularity, the individuals also which reproduce sexually differing materially in form and organization from those which gave rise to them by a non-sexual method; such a condition of affairs is termed Alternation of Generations, a generation of individuals reproducing only by a non-sexual method alternating with a second generation reproducing exclusively or almost so in the sexual manner. Typical examples of this process are afforded by the Discomedusæ, in many of which the individual produced by the development of the ovum is a fixed, cylindrical organism of simple structure, known as a *polyp*, possessing the power of non-sexual reproduction (see Fig. 55). By a series of transverse divisions it gives rise to a linear colony of individuals which in the course of development assume a form very different from that of the parent polyp, becoming more complicated in structure, more highly organized, and free-swimming. These organisms, known as *Medusæ*, are the sexual generation, producing spermatozoa and ova, the latter after fertilization developing a non-sexual generation, a polyp, with which the cycle begins again.

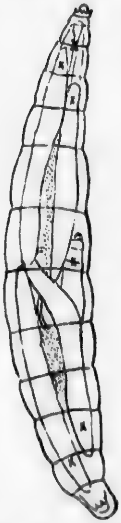
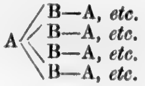
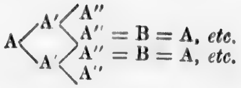


Fig. 29. — Pædogenetic *Cecidomyia* Larva (after Pagenstecher from Hatschek).

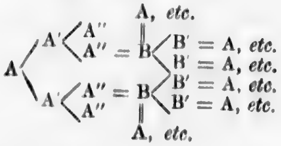
Schematically such an arrangement may be represented thus, A representing the non-sexual and B the sexual generation :



Among the Hydromedusæ, in which group alternation of generations likewise occurs, the process is usually complicated by a number of non-sexual generations succeeding one another before the intervention of the Medusa, thus :



And in some cases the succession is still further complicated by non-sexual reproduction on the part of the medusa, thus :



But such complications do not interfere with the general alternation which invariably occurs in such forms before the completion of the reproductive cycle.

Such a phenomenon as this where a true non-sexual generation alternates with a sexual one presenting a different structure is usually distinguished as *metagenesis* from another form of alternation of generations known as *heterogony*, in which the first generation reproduces parthenogenetically, giving rise to a second generation differing in form from the first and reproducing by the sexual method. Typical examples of this process are to be found among the Trematode worms (q.v.), where the sexual worm gives rise to a sporocyst in the interior of which ova, developing parthenogenetically, give rise to a larva which later on transforms to the adult worm. In a less perfect form heterogony occurs in many lower Crustacea (*Daphnia*), which throughout the warmer portion of the year produce "summer eggs" which develop parthenogenetically, male animals appearing only for a short period in the autumn, as a rule, when the females produce "winter eggs" which develop after fertilization. Here no difference of form exists between the two generations, but such cases, as well as those in which two sexual generations unlike in form and habitat alternate with each other, are usually associated with the more typical examples as instances of heterogony.

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CHAPTER IV.

TRICHOPLAX, THE DICYEMIDÆ AND ORTHONECTIDÆ.

Before passing on to a description of the first type of Metazoa, it will be necessary to consider a few forms which can hardly be assigned to it and yet present too great a differentiation of their component cells to warrant their reference to the Protozoa. A third subkingdom, the *Mesozoa*, has been proposed for them, but until more is known of the relations of some of them at least to other forms the establishment of such a subkingdom seems inadvisable.

Trichoplax adhærens.

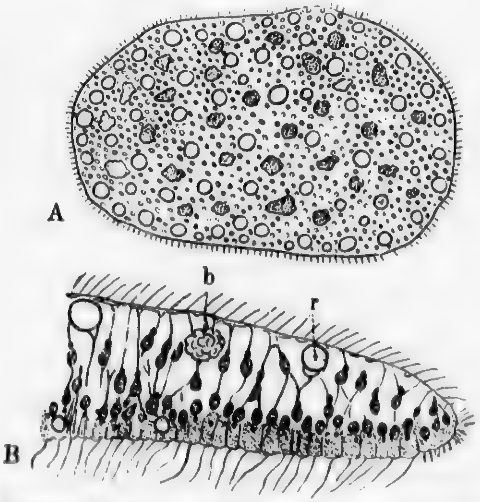

Fig. 30.—*A*, Surface View and *B* Transverse Section through *Tricho plax* (after Schulze).

b = botryoidal structure. *r* = refractive bodies.

In the marine aquaria at Grätz, Vienna, and Berlin there has been found a small organism (Fig. 30, *A*) measuring from

1.5 to 4 mm., but capable of great alteration of form. It is flattened, and creeps about upon the walls of the aquaria in an amœboid manner. It consists, however, of numerous cells (Fig. 30, *B*), the upper surface being covered by a flattened ciliated epithelium, and the lower formed by a layer of columnar cells also ciliated, while the space between the two surfaces is occupied by a network of branching cells, the branches appearing to unite with those of adjacent cells and with prolongations from both the upper and the lower epithelium. The arrangement suggests the three germ-layers ectoderm, endoderm, and mesoderm, but until more is known concerning the reproductive processes such an homology is unwarranted. At present the organism is only known to reproduce by division, and no structures have been discovered which may be identified as ova or spermatozoa. Beneath the upper epithelium, imbedded in the cells of the middle tissue, large refractive spheres (Fig. 30, *B*, *r*) and yellowish-green botryoidal masses (*b*) occur, but they have apparently no connection with reproduction.

THE DICYEMIDÆ.

The Dicyemidæ are elongated vermiform organisms which are parasitic in the renal organs of the Cephalopods. The various species of *Dicyema* (Fig. 31) vary in length from 0.5–7 mm. and are all very simple in structure, consisting of a single elongated central cell (Fig. 31, *C*) extending from one end of the body to the other and covered by a number of ciliated cells arranged in a single layer. Some of these, situated at one end of the body, are smaller than the others and mark off the anterior extremity; there is no mouth or digestive tract and no sense-organs.

Reproduction is carried on by the development of germcells (*g*) produced by the division of the nucleus of the central cell and the concentration around the nuclei so produced of a portion of its protoplasm. The development of these germcells is apparently parthenogenetic and no male *Dicyema* is as yet known. In young individuals the germ-cells segment in the interior of the central cell and give rise to "vermiform" embryos (Fig. 31, *V*) similar to and developing directly into the adult form. Another form of embryo is, however, produced by older individuals, its formation being accompanied by a peculiar behavior of the germ-cells. The nucleus of each one first divides into two unequal parts, the smaller part separating as a paranucleus and undergoing no further development. The germ-cell now segments, and an embryo (Fig. 31, *e*) consisting of a single large cell partially surrounded by smaller cells results. The smaller cells are now thrown off and separate somewhat from each other, and the larger cell repeats the segmentation-process, the smaller cells being again thrown off; and this may happen three or four times, the result being the production of three or four concentric layers of small cells surrounding a single larger one, all lying in the central cell of the parent. The large cell undergoes no further development, but the smaller ones, except those of the last generation, develop into "infusoriform" embryos of a peculiar and complicated structure. The cells of the last generation develop into "vermiform" embryos similar to those found in young Dicyemids.

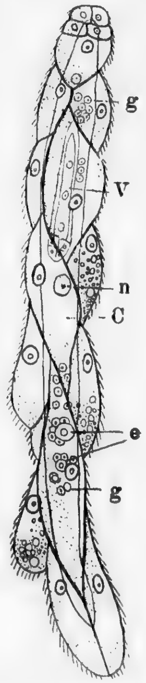

FIG. 31.—*Dicyema typus* (combined from several figures by WHITMAN).

C = central cell.
e = embryos.
g = germ-cells.
h = nucleus of central cell.
V = vermiform embryo.

The fate of the "infusoriform" embryos has not been determined. Since they are ciliated it seems not improbable that they serve for the dissemination of the species and its transference from one Cephalopod host to another. It has, however, been suggested that they may develop into males.

THE ORTHONECTIDA.

The Orthonectids are parasitic on Echinoderms and Nemertean worms and resemble in structure the Dicyemids, the ectoderm consisting of a number of ciliated cells arranged in a single layer and enclosing a mass of germ-cells which correspond to the central cell of *Dicyema*. Between the germ-cells and the ectoderm fine nucleated fibres occur which are presumably muscular.

Three forms of individual are known to occur in the genus *Rhopalura*, one being a male, and the other two females.

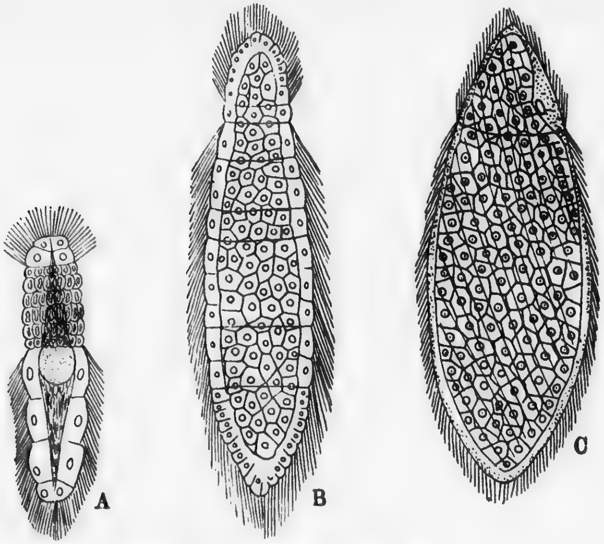

FIG. 32.—*Rhopalura Giardii* (after JULIN).
A, male; *B*, round female; *C*, flat female.

The male (Fig. 32, *A*) is about half the size of the females, which measure about 0.25 mm. in length, and presents a metameric arrangement of the ectoderm which does not extend to the internal cells. The cells of the anterior segment have their cilia directed anteriorly, and are succeeded by a segment consisting of several rows of small non-ciliated cells each containing a refractive body, and behind this there follow three or four segments formed of cells provided with cilia directed backwards. One of the female forms (Fig. 32, *B*) is elongated, and is segmented like the male except that the segments are more numerous and the second non-ciliated segment consists of a single row of cells destitute of refractive bodies.

The other female (Fig. 32, *C*) is, on the contrary, ovoid, flattened, and unsegmented, being ciliated all over; it differs furthermore from the elongated female in possessing on one side near the anterior extremity a granular mass containing a large nucleus whose significance is entirely problematical.

Associated with the difference of form of the two females there is a difference of function. In the elongated form when the ova are mature the anterior two segments split off as a cap and allow the ova to escape, and, on fertilization, these give rise to males. In the ovoid form, however, the ova are imbedded in a gelatinous mass, and are liberated by the breaking up of the parent into a number of fragments; from the ova females of both forms develop.

The systematic position and affinities of the Dicyemidæ and Orthonectidæ is a matter of uncertainty. They have been held by some authors to possess affinities with the Gregarinida and by others to be degenerate flat worms, while others have sought to trace resemblances to the Rotifers. The granular mass with the large nucleus which occurs in the ovoid *Rhopalura* has been supposed to represent a rudiment of a digestive tract, while the superficial metamerism of the male and elongate female of the Orthonectida may possibly point to a derivation from more highly organized ancestral forms. There can be but little doubt that the Dicyemidæ and Orthonectida are closely related, but at present sufficient evidence is wanting to warrant any definite conclusions as to their relationships to other forms.

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CHAPTER V.

TYPE CŒLENTERA.

The Cœlentera include the diploblastic Metazoa, only two germ-layers, the ectoderm and endoderm, being represented in their organization (Fig. 33). Between these two layers, however, a third (Fig. 33, *mg*) is invariably present, which in its primitive condition is not cellular, but consists of a gelatinous or fibrous substance secreted by one of the two cellular layers. Usually, however, cells from the endoderm or ectoderm wander into it, and sometimes are so numerous as to give it the appearance of a cellular layer. Even in such cases, however, the gelatinous matrix is the fundamental substance of the layer, which it seems preferable to term the *mesoglœa*, rather than to imply an homology which does not exist by designating it the mesoderm.

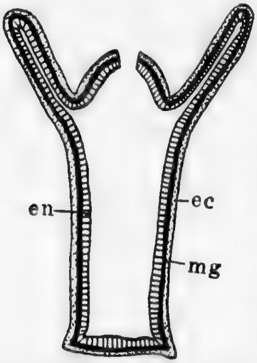

Fig. 33.—Diagram of *Hydra* to show the General Structure of a Cœlenterate.

ec = ectoderm.
en = endoderm.
mg = mesoglœa.

In consequence of the absence of the mesoderm the Cœlenterates present in the interior only a single cavity. Consequently it may be said that the cœlom is not represented in the Cœlentera, though their central cavity is usually regarded as equivalent to both cœlom and enteron of the higher forms. The so-called endoderm, however, seems to be homologous with their mesoderm *plus* endoderm, and may be more accurately termed the *mes-endoderm*, and it seems preferable to regard the cœlom as not yet differentiated.

Another feature which obtains throughout the group is the radiate ground-form. In many but one axis can be determined, and in the Sponges the form may become so irregular that they may be considered to be destitute of axes. In such forms as the Medusæ, however, a typical radiate form occurs, there being two or more similar axes at right angles to the vertical one, and throughout the higher members of the group this radiate symmetry is more or less apparent, though it becomes decidedly obscured in certain Anthozoa by a pronounced tendency towards bilaterality, which in a few forms (*Cerianthidæ*) actually replaces it.

In correspondence with their low grade of general structure there is no very extensive differentiation of tissues. A considerable degree of division of labor of course occurs among the cells, and cells having the same function may be aggregated together so as to form a somewhat definite tissue, as in the case of the nerve, muscle, and reproductive cells, but even in these tissues there seems to be a considerable amount of individuality retained by the constituent cells, and the tissues can only be regarded as exceedingly diffuse. Of organs, except in some colonial forms with division of labor among the constituent individuals, it is hardly correct to speak, the Cœlenterates not having progressed beyond the organ stage of individuality.

The type Cœlentera may be divided into two subtypes, the *Porifera*, or Sponges, and the *Cnidaria*.

I. SUBTYPE **Porifera.**

The Sponges, on account of their fixed life and irregular form, were long regarded as plants, and it is only within comparatively recent times that their true relationships have been ascertained. They are almost exclusively marine in habitat, occurring in large numbers in the warmer seas, and inhabit the ocean depths as well as the shallower waters. A few genera, e.g. *Spongilla*, *Ephyatia*, represented by numerous species, are inhabitants of fresh water.

The simplest Sponges (Fig. 34) have the form of a hollow cylinder fixed at one end, while at the other is an opening, the *osculum*, and scattered over the surface of the cylinder are a number of smaller openings, *prosopyles*. Through these water passes into the central cavity, the cœlenteron, and escapes by the osculum. The exterior of the body is covered by a layer of flat cells, the ectoderm, and the cœlenteron is lined by collared cells provided with a single flagellum and resembling greatly Autoflagellata belonging to the genus *Codosiga*. These cells constitute the endoderm, and between it and the ectoderm is the mesoglœa, in which are imbedded large numbers of cells, giving it almost the appearance of a cellular layer.

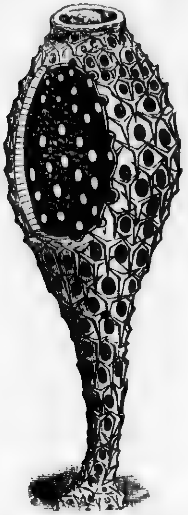

Fig. 34.—An Ascon Sponge, *Ascetta primordialis* (after Haeckel from Sollas).

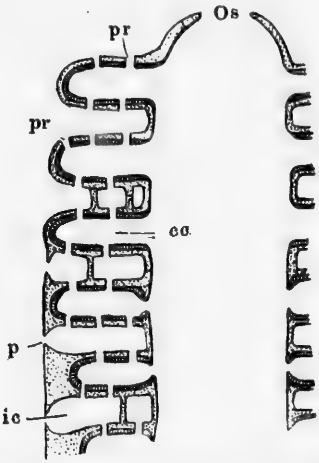

Fig. 35.—Diagram to show the General Structure of a Sycon Sponge.

The upper portion represents the simplest condition, the complexity increasing downwards.

cc = ciliated chamber.
ic = inhalent canal.
Os = osculum.
p = inhalent pore.
pr = prosopyle.

In such simple Sponges the mesoglœa is comparatively thin and the pores open almost directly into the cœlenteron lined by the collared cells. This arrangement constitutes the first or *Ascon* type of structure. In the majority of forms a much greater complexity arises from the walls of the simple cylinder being, as it were, drawn out into a number of finger-like processes, each of which communicates by a wide opening with the cavity of the original cylinder (Fig. 35). The cells lining the central cavity become flattened, the collared cells being found only in the interior of the secondary cylinders which radiate from the central chamber (*cc*). Pores, termed *prosopyles* (*pr*), occur in the walls of the secondary cylinders, which are closed at their free ends. Through these prosopyles water passes into the interior of the radiating cylinders, thence into the central cavity and so to the exterior by the osculum. Further complication occurs by the walls of the radiating cylinders coming in contact with each other and fusing in a more or less irregular manner, the space between the various cylinders being thus divided into a series of more or less well-defined inhalent canals (*ic*) into which the water passes through *pores* (*p*) which lie, morphologically, between the extremities of the radiating cylinders. The cavities of these cylinders now form the ciliated chambers, and Sponges in which they possess the cylindrical form are said to belong to the *Sycon* type. The annexed diagram (Fig. 35) illustrates the different stages of complexity met with in Sycon Sponges.

The next complication consists of the branching of the ciliated chambers, though they still retain a cylindrical shape, and their separation from the central cavity by a tract lined with flattened cells (Fig. 36, *A*); and finally the collared cells become limited to a portion of the radial chambers, the ciliated canals thus becoming circular in shape and united with the central chamber by long and rather slender canals lined with flattened cells (Fig. 36, *B*). This constitutes what is termed the *Leucon* type of structure. In this type the pores upon the surface of the Sponge frequently do not open directly into the canals leading to the ciliated chambers, but into a wide lacunar cavity, the *subdermal space*, lying below the cortical layers of the sponge, and with this the canals communicate.

To these complications of arrangement further complexity is added by the occurrence in many Sponges of what may be considered budding, in some cases leading to the formation of definite branches, or in others producing only a number of oscula, each, however, with its own canal system.

The general characteristics of the ectoderm and endoderm have been indicated in the preceding description of the canal systems; the mesoglœa requires, however, further notice. It consists of a gelatinous matrix which, however, contains large numbers of cells presenting a considerable amount of differentiation. Some are amœboid in form, others contain pigment, others again are elongated and spindle-shaped, forming the contractile cells, others form the reproductive elements, ova and spermatozoa, while others again are skeletogenous in function, well-developed skeletal structures being present in almost all Sponges. In some forms the skeleton presents the form of siliceous spicules either of a simple needle-like form, or presenting modifications of a four- or six-rayed ground-form, or finally assuming the form of hooks, anchors, or spiny spheres. In another group there is, associated usually with needle-like siliceous spicules, a network of a horny material termed *spongiolin* which forms a supportive scaffolding for the soft parts of the Sponge, and lastly, in another group the spicules are composed of carbonate of lime and present a variety of forms (Fig. 36, *A*).

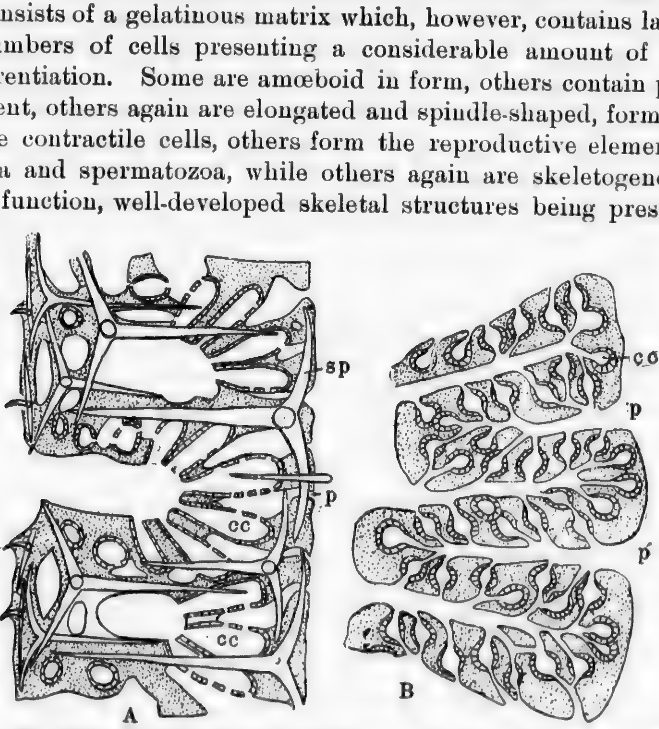

FIG. 36.—TWO FIGURES SHOWING DIFFERENCES IN THE COMPLEXITY OF STRUCTURE OF A LEUCON SPONGE.

A. *Leucilla ater* (after DENDY); B. *Oscarella lobularis* (after SCHULZE).
cc = ciliated chamber. *p* = inhalent pore. *sp* = spicule.

Nerve-cells have also been described, though a definite nervous system cannot be said to exist. Elongated retractile processes have been observed projecting from the surface of certain sponges, and at the base of each is a group of stellate cells each of which sends a long slender prolongation into the process. To these cells a nervous function has been attributed and the processes have been considered sensory; with the exception of these structures, however, no sense-organs or nerve-elements have been yet observed.

The Sponges may be arranged according to the nature of their skeleton, in four orders.

1. Order **Calcarea.**

In the Calcarea the skeleton is always present and is formed of spicules consisting of carbonate of lime. The group contains forms of various complexity of structure, from the simple cylindrical *Leucosolenia* constructed upon the Ascon type through Sycon forms such as *Grantia* to representatives of the third and fourth types. Indeed it is only in this group that the Ascon and Sycon types of structure are found. All the known species are marine and live at only slight depths.

2. Order **Cornacuspongiæ.**

The skeleton of the Cornacuspongiæ consists either of siliceous, needle-like spicules, frequently more or less united by spongiolin, or else entirely of a network of fibres composed of the latter substance. Like the Calcarea they are inhabitants of shallow water and are for the most part marine, though some forms (*Spongilla*, Fig. 37, *Ephydatia*) live in fresh water. These fresh-water forms are of a green color due to chlorophyll, the presence of this pigment being supposed by some observers to depend on numerous unicellular algæ living in the substance of the Sponges. To this group belongs also the Sponge of commerce (*Euspongia*), whose value depends upon the entire absence of siliceous spicules, and which is found in the shallow waters of the eastern portion of the Mediterranean, in the Red Sea, and in the Western Hemisphere in the waters surrounding the Bahama Islands

3. Order **Spiculispongiæ.**

The skeleton in the Spiculispongiæ is occasionally entirely wanting, as in the genus *Halisarca*, but usually consists of siliceous spicules usually tetraxial or rod- or club-shaped, sometimes interlocking with one another so as to form a firm skeleton. One of the members of the group is the "boring sponge," *Cliona*, which excavates channels in and assists in the disintegration of oyster-shells, frequently attacking the shells of living animals and contributing to their destruction.

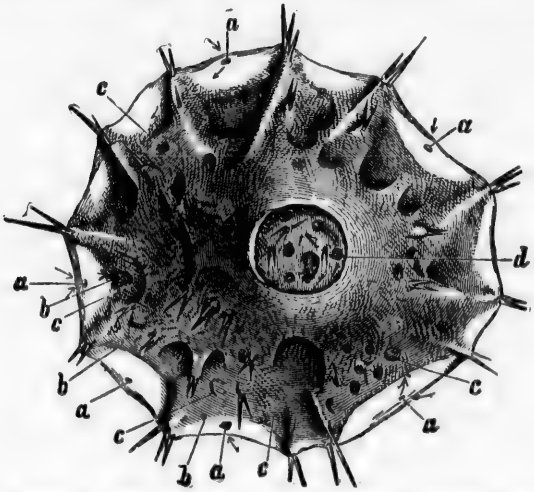

FIG. 37.—A SMALL *Spongilla* WITH ONLY A SINGLE OSCULUM (from HUXLEY).

a = inhalent pore.
c = ciliated chamber seen through the tissues.
d = osculum.

4. Order **Hyalospongiæ.**

The Hyalospongiæ are essentially deep-sea forms, and are characterized by the possession of six-rayed siliceous spicules as skeletal elements. The spicules may become fused together to form a firm siliceous network having the appearance of spun glass, as in the genus *Euplectella*, commonly known as Venus' Flower-basket.

Reproduction of the Porifera.—Sexual reproduction occurs probably throughout the entire group of the Sponges, the reproductive elements, ova and spermatozoa, differentiating from mesoglœal cells. Many Sponges are hermaphrodite, the spermatozoa developing usually somewhat in advance of the ova, but some forms seem to have separate sexes. The ova are fertilized while still within the tissues of the parent and undergo a portion of their development there, later breaking through into a canal and so passing to the exterior as a ciliated free-swimming structure. The segmentation of the ovum in typical cases results in the formation of a blastula, which becomes converted into a solid ciliated sterrula by immigration. After swimming about for a time the sterrula loses its cilia and settles down, a cavity appearing in its interior, which later, in forms which possess ciliated chambers, gives rise to these structures as a series of pouches in connection with which canals arise. The pores and the osculum finally break through, invaginations from the exterior giving rise to the former.

In some forms, however, the blastula stage undergoes invagination, usually of a rather peculiar form, in which case a gastrula results instead of a sterrula. The gastrula settles down and becomes fixed by the pole at which the blastopore occurs, the further development being similar to that found in the immigration types.

In addition to the sexual method most Sponges also possess the power of non-sexual reproduction, dependent on their capabilities for regeneration. A detached portion of a Sponge will, under favorable conditions, regenerate into a new individual, and this power has been applied to the artificial reproduction of the commercial Sponges. In some forms in addition to this a process of internal budding occurs, a number of the mesoglœal cells aggregating together and developing into an oval, ciliated, sterrula-like structure which, leaving the parent, develops into an adult Sponge (*Esperella*). In the fresh-water *Spongilla* this process is carried to the greatest extent, and towards the approach of winter in temperate latitudes completely replaces the sexual method. The internal buds of *Spongilla* are known as *gemmules* and are especially adapted for tiding the species over unfavorable conditions, such as cold or dryness, which the vegetative individual cannot withstand. They are spherical bodies consisting of a mass of cells richly laden with food-matter, and enclosed in a double chitinous wall, with an opening at one point, a number of siliceous spicules, in the allied genus *Ephydatia* of a very characteristic form and known as *amphidiscs*, being arranged between the two layers of the wall. On the approach of cold weather the Sponge dies down and the gemmules thus fall to the bottom of the ponds or streams, where they remain unchanged until the approach of warmer weather, when the internal cellular mass flows out through the pore (which is closed only by a thin membrane) and develops into a new *Spongilla*.

The relationships of the Sponges have long been a matter of discussion. For a long time they were regarded as plants and later as colonies of Protozoa, but the discovery of sexual reproduction in them and of their mode of development demonstrated that they were to be considered Metazoa. At present the question as to whether they are to be associated with the *Cnidaria* among the Cœlenterates or regarded as a distinct type is still open, though the weight of evidence and authority is in favor of their Cœlenterate character. Such simple forms as *Leucosolenia* certainly point in that direction, and, if the occurrence of a sterrula formed by immigration prove the typical mode of development, the embryology of the Sponges presents stages up to the formation of the ciliated chambers which are step by step comparable to what occurs in the *Cnidaria*.

II. SUBTYPE **Cnidaria.**

The *Cnidaria*, like the Sponges, have in their simplest forms the general form of a hollow cylinder open at one end and consisting of but two cellular layers, the ectoderm and endoderm, between which is interposed a fibrous or gelatinous mesoglœa which may or may not contain cells. Differences from the Sponges are found in the occurrence, except in one or two forms, of a number of elongated, contractile processes or tentacles around the mouth of the cylinder (see Fig. 33), and in the absence of inhalent pores upon its surface. Such simple forms are known as *polyps*, and they are usually attached organisms with little or no power of locomotion. A large number of Cnidaria present a very different form, however, being disk- or bell-shaped, a process comparable to the clapper of a bell hanging down from the centre and having at its extremity the mouth-opening. This leads into a central cavity, the cœlenteron, lying in the substance of the bell, and from this pouches or fine canals radiate out towards the rim, where, in some cases, they are united by a circular canal which runs completely round the bell at this region. To the margin of the bell tentacles are usually attached, and sense-organs, presenting frequently considerable complexity of structure, are found in the intervals between the tentacles or at their bases. These forms, known as *medusæ*, are, as a rule, free-swimming, propelling themselves through the water by vigorous contractions of the bell.

All Cnidaria, whether of the polyp or medusa form, possess in their tissues peculiar elements altogether unrepresented in the Sponges. These are the *nematocysts* or so-called thread-cells. Each consists of an oval or spherical cyst (Fig. 38, *c*) with a membranous wall and fluid contents, the wall being prolonged at one end into a long, exceedingly delicate, hollow, thread-like filament sometimes furnished with spines at its base, and, in an undisturbed cyst, is invaginated, and coiled up in the interior (Fig. 38, *t*). These nematocysts are produced by and enclosed within special cells known as *cnidoblasts* (*cn*) lying principally in the ectoderm, and in their most highly developed form differentiating below into a supporting stalk (*s*) which rests upon the outer surface of the mesoglœa. From the outer extremity there projects beyond the surface of the ectoderm a short hair-like process, the *cnidocil* (*cl*), and, in addition, an exceedingly fine process of some length (*n*) is given off at the junction of the stalk with the cyst-containing portion of the cell. These two processes are supposed to be sensitive, the longer one perhaps bringing the cnidoblast into connection with nerve-cells lying elsewhere in the ectoderm. In some way not yet properly understood, a stimulation, such as a touch by some foreign

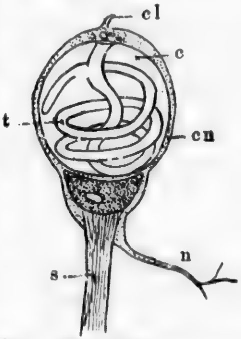

Fig. 38. — Nematocyst Cell of *Physalia*.

c = nematocyst.
cl = cnidocil.
cn = cnidoblast.
n = nerve prolongation.
s = supporting process.
t = thread.

body, produces an evagination of the coiled thread from the cyst, in the interior of which it has been bathed by the fluid contents. The evagination is of sufficient force apparently to puncture the skin of many animals and so inoculate the contents of the cyst, which are of a poisonous nature, and produce inflammatory disturbances, and in minuter organisms paralysis or death. To the presence of these structures jelly-fishes owe their stinging powers, and they form efficient weapons both for obtaining food and for warding off enemies.

The Cnidaria may conveniently be divided into three classes:

I. Class *Hydromedusæ.*
II. " *Scyphomedusæ.*
III. " *Anthozoa.*

I. CLASS **HYDROMEDUSÆ**.

The Hydromedusæ present both polyp and medusa forms, the members of some of the orders contained within the class being only of the medusa form, while in another order only the polyp form occurs. Usually, however, both forms occur in more or less perfect development, representing two stages in the life-history of an individual and succeeding one another in the definite manner which has been already described as an alternation of generations. The polyps possess the power of non-sexual reproduction by budding and give rise by this method not only to medusæ, but also to other polyp individuals which may remain in connection with one another and thus give rise to branching colonies. As a rule, the medusa individuals separate from the polyp and lead a free life, but in the order *Siphonophoræ* they may remain in connection with each other and with polyp individuals, undergoing various adaptations of form in accordance with different functions which they assume, the whole forming a colony presenting in a high degree a division of labor among the component individuals.

As has already been pointed out the structure of the polyp form differs considerably from that of the medusa. The polyp is more or less cylindrical in form, tapering off above

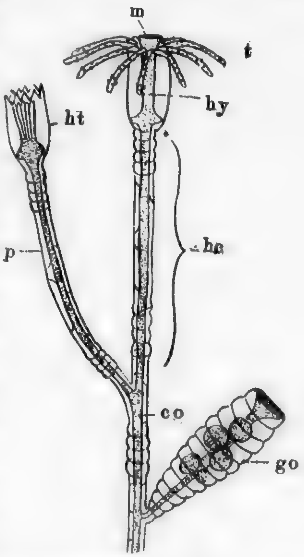

FIG. 39.—PORTION OF A COLONY OF THE CAMPANULARIAN HYDROID *Clytia*

co = cœnosarc.
hc = hydrocaulus.
ht = hydrotheca.
hy = hydranth.
go = gonotheca.
m = mouth.
p = perisarc.
t = tentacle.

so that the free end has a somewhat conical shape, the mouth being situated at the end of the cone. At the base of the cone, which is termed the *hypostome*, there is usually a circle of tentacles, though occasionally they are scattered irregularly over the surface of the hypostome, and a second circle of tentacles may be present at the base of the polyp (*Pennaria*). In colonial forms each individual (*hydranth*) (Fig. 39, *hy*) is situated at the extremity of a stalk or *hydrocaulus* (*hc*), the various stalks either uniting together to form a branching colony or else arising from a network, the *hydrorhiza*, which covers the surface upon which the colony grows; or occasionally each hydranth arises, without the intervention of a hydrocaulus, from a flat plate-like expansion common to all. In either case the cœlenteron is continuous throughout the entire colony, the fleshy substance of the hydrocaulus and hydrorhiza, *cœnosarc* (*co*), being tubular and in direct continuity with the body-walls of the hydranths. The cœnosarc is enclosed within a chitinous substance termed the *perisarc* (*p*) secreted by the ectodermal cells and sometimes prolonged at the end of each hydrocaulus into a cup-like structure, the *hydrotheca* (*ht*), into which the hydranth may be retracted; occasionally this ectodermal secretion takes the form of carbonate of lime.

The ectoderm generally shows a considerable amount of differentiation of its constituent cells. In addition to the *cnidoblasts*, which have been already described (p. 77), with lio-muscular, muscular, glandular, and nerve cells are generally to be found in it. The epithelio-muscular cells (Fig. 40, *A*) are the most numerous and consist of columnar cells, one extremity of which bears a cilium and helps to form the outer surface of the body, while the other is prolonged into a somewhat spindle-shaped process of highly contractile muscular substance. The muscle-cells (Fig. 40, *B*) are modifications of these, having lost their connection with the surface of the body, the cell-protoplasm and nucleus forming a small elevation on the muscle-fibre. The muscle-fibres rest upon the outer surface of the mesoglœa, and in the ectoderm are, as a rule, arranged longitudinally, so that by their contraction they cause a shortening or retraction of the polyp. The nerve-cells are of two kinds: (1) sensory cells (Fig. 40, *C*), which are slender cells whose free end bears a single cilium, while the inner end is produced into one or more slender nerve-processes which are supposed to place these cells in connection with (2) the ganglion-cells. These are stellate cells lying in the deeper layers of the ectoderm, just external to the muscle-cells, and sending off delicate processes in various directions so as to form a plexus of nerve-fibres ramifying through the ectoderm.

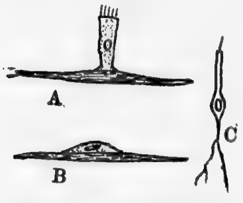

FIG. 40.—*A* = Epithelio-muscular cell of Cœlenterate; *B* = muscular cell; *C* = sensory cell.

The mesoglœa is thin and more or less fibrous in structure, and rarely contains cells. The endoderm-cells are large and are of the epithelio-muscular variety, the muscle-fibres having a circular arrangement producing by their contraction a diminution of the diameter of the polyp. The protoplasmic portion of each cell is furnished with a single flagellum and is digestive in function, taking food-particles into its substance and there digesting them. In addition to these, glandular cells also occur in the endoderm, especially in the region of the hypostome.

The medusa forms have the shape of a bell (Fig. 41) which may be either shallow or deep, the mouth of the bell in all cases being partially closed by a fold of tissue which projects from the rim, and is known as the *velum*; from the presence of this structure these medusæ have been termed *craspedote* medusæ. The cavity between this and the bell is the *subumbrellar cavity*, into which projects a process corresponding to the clapper of the bell and termed the *manubrium*. At the free end of this is the mouth, which opens into a canal traversing the manubrium and communicating at its base with the gastric cavity lying in the substance of the bell. From this four (in some cases more) canals or pouches radiate out towards the rim and communicate there with a circular canal which extends completely round the margin of the bell, just where the velum joins it. The canal of the manubrium, the gastric cavity, and the radiating and circular canals together constitute the cœlenteron. To the margin of the bell tentacles, varying in number, are generally attached, on or between the bases of which sense-organs are to be found.

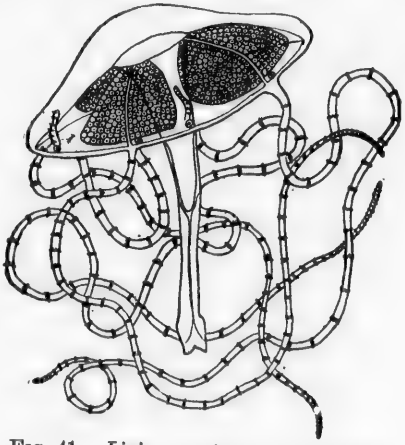

FIG. 41.—*Liriope scutigera* (after BROOKS).

The medusæ differ not only in form but also in habit from the polyps, being free-swimming organisms, propelling themselves through the water by expelling the water from the subumbrellar cavity through the velar opening by sudden and rhythmical contractions of the bell. In accordance with this free mode of life sense-organs are present, and a higher development of the nervous system than is found in the polyps obtains. The sense-organs vary both in structure and function in different medusæ, in some being spots of pigment sometimes provided with a refractive lens and functioning as light-percipient structures. Such medusæ (Fig. 45) are termed *ocellate*, or, since the eyes are on the surface of the bell and are not enclosed within a chamber formed by the growth around them of the adjoining tissues, they are sometimes termed *gymnophthalmatous*. In other forms again the sense-organs consist of a group of cells containing in their interior crystals of carbonate of lime and having a somewhat vesicular appearance, and in the neighborhood of these are sensory cells with long stiff cilia to which are imparted any vibrations which the crystals may manifest. Such crystal-containing cells are known as *otocysts*, on the supposition that they form auditory organs, but it seems more probable that their function is that of equilibrium organs, informing the medusæ of their position. Medusæ possessing such organs (Fig. 43) are termed, to distinguish them from ocellate forms, *vesiculate* medusæ.

The ectoderm which covers the outer surface of the bell is much flattened, but near the rim it becomes columnar and is ciliated, some of the cells assuming the form of sensory cells similar in appearance to those of the polyps, their slender nerve-filaments forming a delicate plexus in the deeper layers of the ectoderm, in which are here and there imbedded stellate ganglion-cells. A special nerve-ring surrounds the bell at its margin. The ectoderm-cells which cover both surfaces of the velum and the subumbrellar surface are of the epithelio-muscular and muscular types, the muscle-fibres being for the most part arranged circularly. In the deeper layers of the subumbrellar ectoderm numerous ganglion-cells with long prolongations occur forming a network immediately external to the muscle-processes, and at certain definite regions collections of reproductive cells occur.

The mesoglœa of the subumbrellar surface and of the velum is thin, resembling that of the polyps, but in the convex portion of the bell it is very thick and gelatinous in texture, and may in some cases contain cells. The endoderm is throughout the cœlenteron ciliated; in the tentacles, which may be either hollow or solid, it may retain its ciliated character, or else in the solid tentacles form a solid axis similar to that of the tentacles of the polyp forms.

Such are the general structural features common to all the Hydromedusæ. It remains to add here certain points by which especially they are distinguished from other groups of Cnidaria. These are: (*a*) the ectoderm and endoderm meet at the mouth-opening; (*b*) the sense-organs when present are never modified tentacles: (*c*) a velum is always present in the medusa forms; and (*d*) the reproductive elements have their origin in the ectoderm.

1. Order **Hydrariæ.**

To this order belongs the *Hydra*, a common inhabitant of fresh-water ponds and streams in all parts of the world. It is a simple cylindrical organism, adherent by one extremity to foreign bodies, though not fixed, being able slowly to change its position. Below the short hypostome is a single row of exceedingly extensible tentacles, which are hollow, a peculiarity found in no other Hydromedusan polyps. So long as conditions are favorable and nutrition abundant *Hydra* reproduces by budding, the buds separating from the parent form after a certain period of growth. Sexual reproduction also occurs, the spermatozoa developing in the ectoderm a little below the ring of tentacles, while the ova form in the same layer somewhat lower down on the body, the animals being hermaphrodites. The ova after fertilization remain imbedded in the ectoderm of the parent for some time, but later, developing around them a cyst, they sink to the bottom of the water, and there remain usually for some time without developing further. In this condition they are able to withstand a considerable amount of cold and dryness, and so may tide the species over unfavorable conditions. No medusa stage occurs in *Hydra*.

Hydra grisea L. is a brown form, relatively large in size, while *H. viridis* L. is smaller and of a dark-green color due to chlorophyll-containing corpuscles imbedded in the ectoderm-cells and supposed by some authors to be unicellular Algæ of a symbiotic habit. (See p. 20.)

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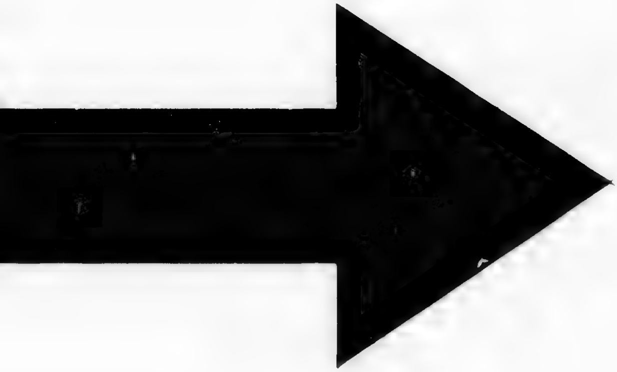

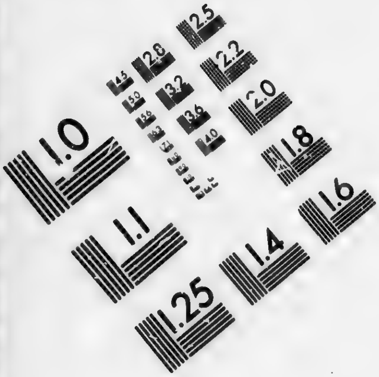
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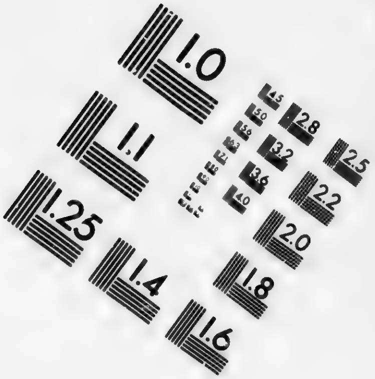
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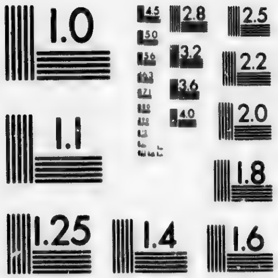
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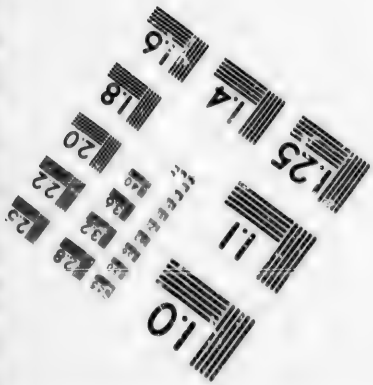
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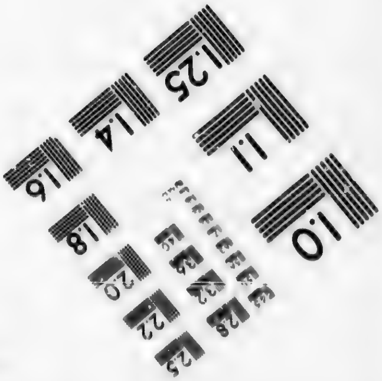
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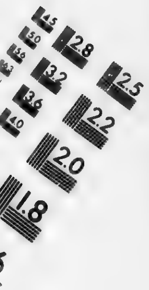
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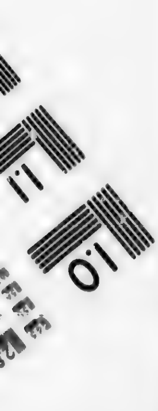
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2. Order **Narcomedusæ.**

In the Hydrariæ the polyp form occurs without a medusa, in the order *Narcomedusæ* the reverse is the case, since in it the medusa form is the only one present in a typical state of development. The medusæ are usually somewhat lens-shaped structures (Fig. 42), with a lobed margin, the velum (*v*), instead of being horizontal, being pendent from the margin (*m*) and extending up in the intervals between the lobes. At the apex of each one of these intervals is situated a short, stiff, solid tentacle which is usually bent backward over the exumbrellar surface and is tipped by a knob of nematocysts.

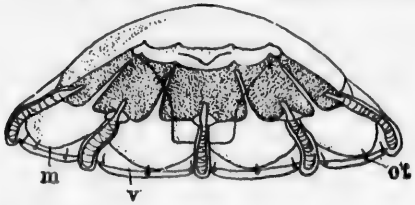

FIG. 42.—*Cunoctantha octonaria* HAECK. (After BROOKS).
m = margin of bell. *ot* = otocyst. *v* = velum.

The cavity of the short manubrium leads into a gastric chamber which is prolonged out towards the margin into broad pouches which lie opposite the tentacles and the intervals between the lobes, and around the margin, following the edge of the lobes and therefore having a festooned arrangement, runs a narrow circular canal which communicates with each radial pouch at the apex of each interlobular interval. This structure is, however, absent in the American species *Cunoctantha octonaria*. The reproductive organs develop in the subumbrellar ectoderm covering the pouches and sometimes extend on to the manubrium. Around the margin of the lobes are seated club-shaped projecting otocysts (*ot*) composed of an external layer of ectoderm surrounding a number of endodermal cells, one or more of which contain a crystal of carbonate of lime. The ectoderm cells in the neighborhood are largely sensory and provided with long cilia, their inner ends contributing to the formation of the marginal nerve-ring.

3. Order **Trachymedusæ.**

In this order only the medusa form is present and it resembles in many respects that of the Narcomedusæ. The bell is somewhat flattened, but is not lobed at the margin; while the velum has the usual horizontal position and the long slender manubrium projects some distance outside of the subumbrellar cavity. From the gastric cavity four, six, or eight radiating canals arise, which join at the margin the circular canal, and in the ectoderm of the subumbrellar surface over a small area along the line of these canals the reproductive cells develop. At the margin a number of sense-organs, otocysts, are present, agreeing essentially in structure with those of the Narcomedusæ and are sometimes projecting or in other cases more or less enclosed in a cavity formed by the growing up around them of the adjacent substance of the bell. The tentacles vary somewhat in shape and structure in different genera. In *Rhopalonema* they are all solid, eight being somewhat longer than the other eight at whose bases are the otocysts; in *Liriope* (Fig. 41) four, situated opposite the radiating canals, are hollow and extensible, while the other four are solid and bent back over the exumbrellar surface as in the Narcomedusæ; while in *Geryonia* all the six tentacles are hollow.

4. Order **Campanulariæ or Leptomedusæ.**

In this order both the polyp and the medusa form occur in the life-history of the individual, alternation of generations being the rule. The polyp generation takes the form of a branching colony, which generally shows a certain amount of division of labor among the component individuals. The nutritive hydranths or *trophopolyps* present the typical form already described (p. 78), and each is seated in a cup of perisarc, the *hydrotheca*, into which the polyp may retract. Such polyps reproduce only polyp forms, but in addition others destitute of mouth and tentacles, and known as *gonopolyps*, occur, which produce by budding numerous medusæ or medusoid buds, the polyp and its progeny being together enclosed in a cup of perisarc, differing in shape from the hydrotheca and known as the *gonotheca* (Fig. 39, *go*). On account of the presence of these cups the polyps of this order are sometimes termed *calyptoblastic*. In the typical Campanularian polyp colonies, such as those of *Eucope* or *Obelia*, no further differentiation of the polyps is found, but in the family Plumularidæ in the neighborhood of each of the small hydrothecæ there are one or more slender extensible polyps lacking mouth and tentacles whose endoderm is a solid axial cord, while the ectodermal cells send off long, streaming, pseudopodia-like processes, these polyps apparently playing the part of food-providers for the colony.

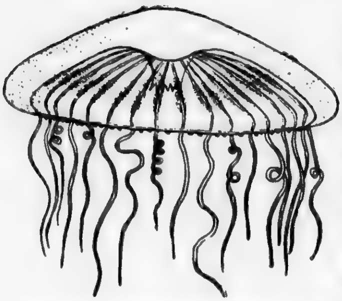

FIG. 43.—*Rhegmatodes tennis*, Ag.

The medusæ (Fig. 43) are usually very shallow bells, with numerous hollow tentacles depending from the margin, and resemble the Trachymedusæ in that the reproductive organs develop on the line of the radiating canals. Of these there are in the majority of cases four, though occasionally, as in *Æquorea*, they may be very numerous. Sense-organs are always present at the margin of the bell and, as in the Trachymedusæ and Narcomedusæ, are always otocysts, the medusæ belonging to the vesiculate category. A marked difference obtains between the otocysts of the Leptomedusæ and those of the two preceding orders in that the calcareous crystals are in the former developed in ectoderm cells. The otocysts furthermore primitively occur on the inner surface of the velum, where they are lodged in a slight depression, which may, however, deepen so much that the otocysts appear to be imbedded in the substance of the bell.

In the typical Campanularians free-swimming medusæ are developed, and according as the polyps or the medusæ attract especial attention the order may be termed that of the Campanulariæ or that of the Leptomedusæ. In a few forms, such as *Rhegmatodes*, up to the present no polyp generation is known to occur, and conversely in certain genera, such as *Ser-*

tularia and *Halecium*, and in the Plumularidæ, e.g. *Aglaophenia*, it would appear at first sight that no medusa generation occurred. This, however, is not strictly accurate, the appearance depending on the medusa-buds in these forms never becoming free-swimming but remaining in a more or less undeveloped condition, the ova and spermatozoa becoming mature notwithstanding the imperfect development of the medusæ. Alternation of generations, however, exists in these forms just as much as in the typical Campanularians, for, no matter how degenerate the buds of the gonopolyps may be, they must still be regarded as the medusa generation.

5. Order **Tubulariæ** or **Anthomedusæ.**

In this order, as in the preceding one, a well-marked alternation of polyp and medusa generations occurs. The polyps are united to form colonies, the individual hydranths being constructed on the Tubularian type, i.e. the perisarc ceases at the base of each hydranth so that there is no hydrotheca. The tentacles show a greater variety of form and structure than in the Campanularian forms, and, though sometimes filiform and arranged in a single cycle at the base of the hypostome (*Margelis*), are yet in other forms scattered irregularly over the surface of the hypostome (*Clava*), or may be club-shaped (*Coryne*), or in addition to scattered club-shaped tentacles a circle of filiform ones may occur at the base of the hydranth as in *Pennaria*. A division of labor is not the rule as in the Campanularians, but nevertheless this phenomenon is in some cases carried to a much greater extent than in that group. In some forms special *gonopolyps* are present from which all the medusæ arise, but more frequently any of the hydranths may produce these structures. The gonopolyps when they occur are never enclosed within a gonotheca, and hence the term *gymnoblastic*, frequently applied to the polyps of this order. In the genus *Hydractinia* (Fig. 44) a complicated division of labor occurs. The various hydranths composing the colony arise from a flat expansion common to all and formed by the fusion of an original network of cœnosarcal tubes, and on the surface of which numerous stout spines occur. Some of the hydranths are typical trophopolyps (Fig. 44, *tp*) with filiform tentacles and a mouth, but among them are gonopolyps (*gp*) with short-knobbed tentacles below which the medusa-buds arise. In addition there are also towards the periphery of the colony much longer slender hydranths without a mouth and like the gonopolyps in having short-knobbed tentacles, but differing from them in their greater length and in never producing medusa-buds. Finally, in a European species of the genus a fourth exceedingly long polyp (*mp*), destitute of both mouth and tentacles, but furnished at its free end with numerous nematocysts, occurs. These third and fourth varieties of polyp probably are offensive and defensive in function, procuring food for the colony and warding off some predatory enemies.

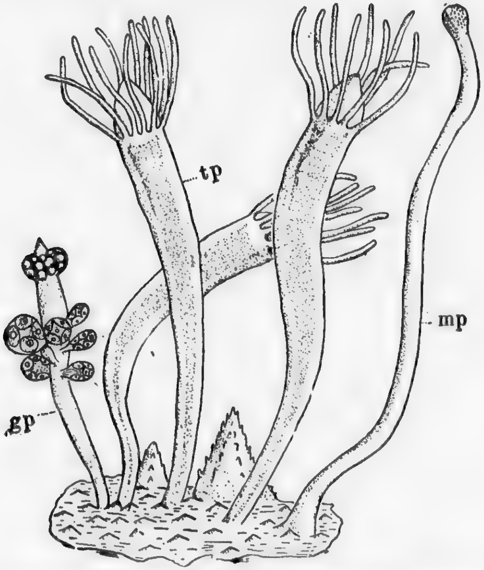

FIG. 44.—PORTION OF COLONY OF *Hydractinia echinata* (adapted from figure by HINCKS).

gp = gonopolyp. *mp* = offensive polyp. *tp* = trophopolyp.

The Anthomedusæ, as the medusa forms are termed, have much deeper bells than the Leptomedusæ, and differ from the latter in that the sense-organs are light-percipient in their function, whence the medusæ are frequently termed *ocellate*, and, secondly, in that the reproductive organs develop in the wall of the manubrium instead of on the line of the four radiating canals. Tentacles as a rule occur at the margin of the bell, and it is at their bases that the eyes are formed. Occasionally, as in *Margelis* (Fig. 45), tentacles also arise from the end of the manubrium. As a rule, the sexual generation is composed of free-swimming medusæ, as in *Coryne*, *Margelis*, and *Pennaria*, but not infrequently the medusa-buds become retarded in their development, as in *Hydractinia*, *Clava*, *Tubularia*, and to an extreme extent in *Eudendrium*, and all intermediate stages between the two extremes are to be found.

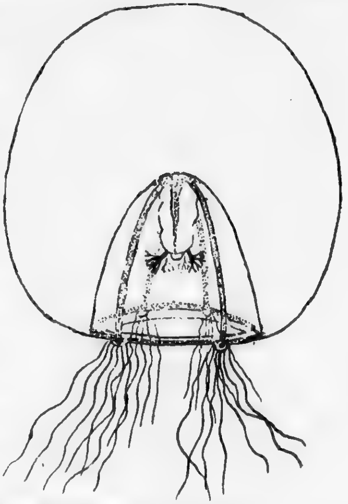

FIG. 45.—MEDUSA OF *Margelis carolinensis.*

6. Order **Hydrocorallinæ.**

The Hydrocorallinæ are colonial marine forms represented by the Stag's-horn Coral, *Millepora*, and characterized by the densely ramified cœnosarcal tubes being enclosed in a mass of carbonate of lime secreted by the cœnosarcal ectoderm and taking the place of the perisarc. From minute pores on the surface of this calcareous mass, the *corallum*, the hydranths protrude and present a well-marked polymorphism. The pores are arranged in groups consisting of a central one surrounded by a varying number of smaller ones. From the central pore protrudes a hydranth with a circle of short tentacles tipped with knobs containing numerous nematocysts; this is the trophopolyp or *gasterozoid* (Fig. 46, *g*). From the smaller surrounding pores more elongated hydranths protrude, destitute of a mouth, and with short scattered tentacles also knobbed; these are probably offensive polyps, of use to the colony in obtaining food, and are known as *dactylozoids* (Fig. 46, *d*). The cavities in the corallum in which the gasterozoids live are divided by transverse partitions into chambers into the outermost of which the hydranth may be retracted, the arrangement recalling what occurs in the corallum of the fossil Tabulate Corals. In the genus *Stylaster*, however, which forms a rose-red branching corallum, these partitions are wanting, a calcareous cone, the *columella*, projecting upwards from the floor of the cavity.

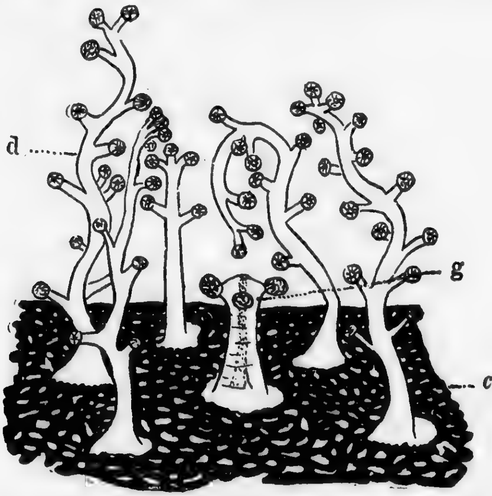

FIG. 46.—PORTION OF COLONY OF *Millepora* (after MOSELEY).
co = corallum. *d* = dactylozoid. *g* = gasterozoid.

In one species at least of *Millepora* a well-marked and typical alternation of generations occurs, medusæ being formed which are set free and develop the reproductive elements in the ectoderm of the manubrium. In the majority of the members of the order, however, the medusa-buds are never set free, and are usually much degenerated, and indeed in *Millepora alcicornis* they may be said to have completely disappeared, and with them the alternation of generations. The medusa-buds develop on the walls of the cœnosarcal tubes, and lie in cavities in the corallum which open to the exterior by a pore through which the egg-embryos escape.

7. Order **Siphonophoræ.**

The Siphonophores are free-swimming Hydromedusan colonies, the constituent individuals of which show a high degree of division of labor. The various forms of individuals which are to be found in different members of the order are usually not present in any one colony, some genera possessing some forms which others lack; it will be convenient, therefore, to consider an ideal form in which the various modifications are present. Each colony (Fig. 47) consists of an axis or stolon on which the various individuals are seated and which places them in connection with each other; it is usually long and slender, but in some cases, as in *Porpita*, may be reduced to a disk. At the extremity of the stolon may be found a float or *pneumatophore* (Fig. 47, *p*), a double-walled sac containing air in the interior, and which is to be regarded as a modified medusa form. Next to it come usually several medusa forms lacking manubrium, tentacles, and sense-organs, and possessing a locomotor function; these are the swim-bells or *nectocalyces* (*n*). At intervals along the rest of the stolon are situated groups of individuals, each group covered over by one or more scale-like structures (*cs*), which are again highly modified medusæ, and in each group is to be found a *trophopolyp* (*tr*), a vase-like polyp form with a wide trumpet-shaped mouth, and having near its base a single tentacle (*t*) which bears along one side a row of numerous secondary

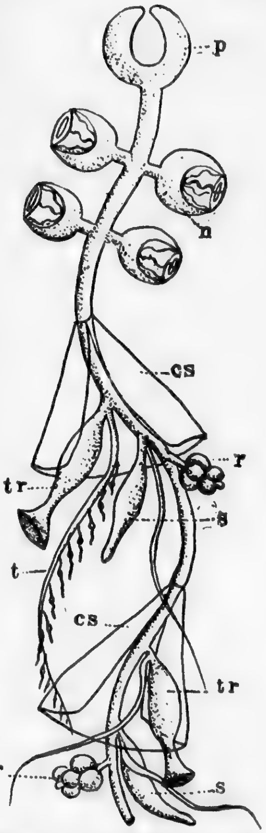

Fig. 47.—Diagram of a Siphonophore Colony.

cs = covering scale.
n = nectocalyx.
p = pneumatocyst.
r = reproductive polyp.
s = sensory polyp.
tr = nutritive polyp.
t = tentacle.

branches, each richly provided with nematocysts. Associated with this nutritive individual is usually a reproductive form, which in some cases may take the form of an Anthomedusa, separating from the colony and leading a free life, as in *Velella*, or may be medusoid, presenting a medusa form, but lacking a mouth and tentacles and never separating from the colony, or finally a gonopolyp (*r*) may occur which bears numerous much-degenerated medusoid buds. In some forms there is still another form of individual (*s*), resembling a trophopolyp, but being destitute of a mouth and having a simple tentacle without the secondary branches. From its great sensibility to stimuli this is supposed to be a sensory polyp.

In some forms, such as *Diphyes*, no pneumatophore occurs, but nectocalyces are present; in others, as *Agalma*, both occur and the colonies resemble somewhat the diagrammatic form described; while in a third group, including the Portuguese man-of-war *Caravella*, the pneumatophore becomes largely developed and nectocalyces are wanting, the stolon at the same time being contracted to a disk lying on the lower surface of the pneumatophore. In *Velella* and *Porpita* the stolon is reduced to a disk, but the pneumatophore is wanting.

Alternation of generations of a typical form, complicated, however, by the polymorphism, occurs in such forms as *Velella*, which possess a free-swimming medusa; in the majority, however, it is obscured, as in many Tubularian hydroids, by the greater or less degeneration of the medusa An alternation of another kind, however, occurs in some forms, the bunches of individuals separating from the stolon and leading for a time an independent existence, during which their medusoid reproductive individuals become mature.

The complicated polymorphism of the Siphonophore colonies leads to a merging of the individualities of the component individuals in that of the entire colony, a process which reaches its highest pitch in such forms as *Velella*. The various polyp and medusa forms of the colony may be considered as organ-individuals, and by their integration an individuality of a higher grade—a metamere-individual—is produced.

Development of the Hydromedusæ.—It has been mentioned as one of the characteristic features of the Hydromedusæ that the reproductive elements arise in the ectoderm. They reach their maturity in the medusæ or medusoid buds except in the Hydrariæ, in which this stage is entirely wanting, and in certain Hydrocorallinæ, in which it has disappeared, and may likewise first become differentiated in the medusa. In many forms, however, in which an alternation of generations occurs they arise in the polyp, sometimes at a point far distant from where the medusa-buds will arise, and reach these structures only after, it may be, a rather extensive series of wanderings. Thus, to take an extreme case, in *Eudendrium* the ova arise in the ectoderm of the main stem of the pinnately branching colony a short distance below the terminal hydranth; as new branches are formed in this same region the young ova migrate into them, passing through the supporting layer and wandering among the endoderm cells. Later on when the gonopolyps arise on the lateral branches the ova wander into them, still in the endoderm, and finally when the medusa-buds develop on the gonopolyps the ova continue their endodermic course into them and eventually, again passing through the mesoglœa, take up their final position in the medusoid ectoderm. Gradations between such an extensive migration and cases in which none occurs are to be found, and it may be stated as a general rule that the more the medusoid buds depart from the medusa form the greater is the migration undergone by the reproductive cells.

As a rule the Hydromedusæ are of separate sexes, the separation affecting the entire colonies—or, to put it slightly differently, the medusæ are always unisexual, and a polyp colony when it occurs gives rise to medusæ or medusoid buds all of the same sex. The Hydrariæ, however, are exceptions to the rule, being hermaphroditic.

A blastula results from the segmentation of the ovum, and this is converted into either a sterrula by immigration or a diblastula (i.e. a hollow two-layered organism without mouth or tentacles) by delamination (see p. 55). If a sterrula be formed, it assumes the diblastula condition by a hollowing out of the central mass, and after swimming about for some time in this condition, if a polyp is to be formed, it settles down upon some foreign body, a mouth breaks through and tentacles appear, producing the first hydranth.

In some forms, such as *Hydractinia*, the free-swimming embryo when it settles down becomes converted into a flat plate-like expansion without mouth or tentacles, from which, as a bud, the first hydranth arises.

If, however, the ovum develops directly into a medusa, as in the Trachymedusæ and Narcomedusæ, the breaking through of the mouth and the formation of tentacles takes place while the embryo is still free-swimming, and the stage so produced may resemble closely a free-swimming hydranth, as in *Cunoctantha*, or may, by the great development of mesoglœa at the extremity opposite the mouth, assume a rather globular form, as in *Liriope*. As the tentacles develop and the bell becomes differentiated by the extension laterally, as it were, of the embryo, the velum arises at the margin of the bell. At this time the cœlenteron is a flattened cavity extending to the margins of the bell, but later it becomes obliterated along four lines, and the obliteration of the cavity extending, the radiating and circular canals and the gastric cavity alone persist, a layer of endoderm-cells sometimes joining them and representing the obliterated portion of the cœlenteron, though often this also disappears.

In the Anthomedusæ and Leptomedusæ, in which the medusæ arise by budding from the polyps, the buds are at first tubular outgrowths of the body-wall (Fig. 48, *A*). The ectoderm at the tip of the bud thickens, depressing the central portion of the endoderm (Fig. 48, *B*), and on the appearance of a cavity in the thickened ectoderm, the subumbrellar cavity, the central endoderm pushes out into the cavity, carrying with it the ectoderm covering it and forming the manubrium (Fig. 48, *C*). In this stage the bud, though still lacking mouth and tentacles, is comparable to the polyp stage of the medusa of direct development at least so far as the cœlenteron is concerned, and by processes identical with those occurring in the directly developing embryo the radiating and circular canals are formed (Fig. 48, *E*), and on the formation of a mouth at the extremity of the manubrium and the development of tentacles the medusa is perfectly formed.

In many cases, however, as already stated, the medusa-buds never reach their complete development, but become sexually mature while still imperfect in form. The stage at which development ceases varies in different forms; in *Tubularia*, for instance, the medusoid bud resembles a medusa except that it lacks tentacles, sense-organs and mouth, and is not free-swimming; in *Clava* not only does development cease at an earlier stage, but a certain amount of degeneration

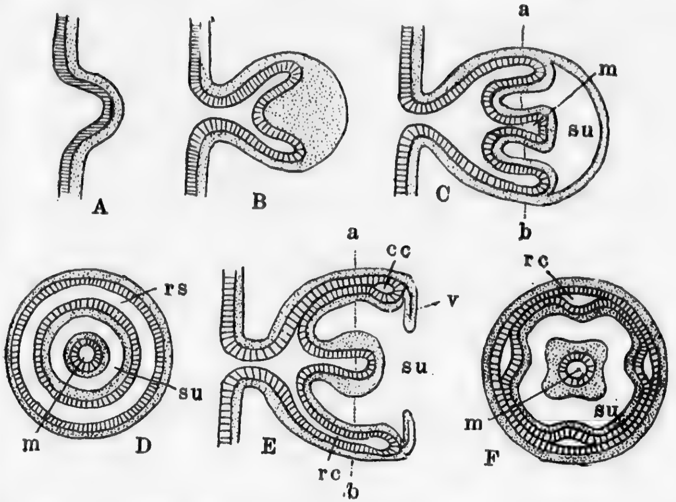

FIG. 48.—DIAGRAMS SHOWING THE DEVELOPMENT OF A MEDUSA-BUD.

A, outpushing of body-wall of polyp; *B*, thickening of ectoderm; *C*, formation of subumbrellar cavity; *D*, transverse section through *C*, along the line indicated by *ab*; *E*, formation of radial canals; *F*, transverse section through *E*, along the line indicated by *ab*.

cc = circular canal.
m = cavity of manubrium.
rc = radial canal.
rs = radial pouch.
su = subumbrellar cavity.
v = velum.

occurs, the rudimentary subumbrellar cavity never communicating with the exterior and the radiating and circular canals being entirely obliterated; and finally in *Eudendrium* the bud never develops beyond the earliest stage in which it is a simple tubular outgrowth of the body-wall.

The Relationships of the various Orders to one Another.—Since the Hydrariæ show such a simple type of organization it is generally supposed that they represent more or less closely a primitive ancestral form, though their usual habitat in fresh water suggests the possibility of their having undergone some degradation. On the supposition that they represent the primitive Hydromedusan the medusa form has been regarded as a secondarily specialized reproductive organ, which in the Narcomedusæ and Trachymedusæ has become so important that the ancestral polyp form is practically suppressed in the life-history. On this view it must be supposed that organisms so similar as the medusæ of the Tubularian and Campanularian polyps have been developed entirely independently of one another, a view which carries with it many difficulties, and that the medusoid buds represent stages in their evolution.

It seems more probable, however, that, leaving the Hydrariæ out of the question, in all the other groups the medusa was the parent form. This is borne out by the fact that in the Narcomedusæ, which, with their broad pouch-like extensions of the gastric cavity, are the most primitive of all the craspedote medusæ, there is no fixed polyp form. It has been shown, however, that the Narcomedusæ and Trachymedusæ in their development pass through a stage which may be considered to represent the polyp form, and if, while in this form, non-sexual reproduction should have taken place, the buds resembling the immature form which gave rise to them, a polyp colony would result, some of the buds of which might continue their development and become medusæ. By this view the difficulties presented by the similarity of the medusæ throughout all the groups where they occur are overcome and the medusoid buds are regarded as imperfectly developed or degenerate medusæ. Furthermore this view is rendered more than probable by the development of *Cunoctantha* and the allied *Cunina*. The former while in the embryonic polyp form actually does bud (Fig. 49), the buds resembling the original embryo which gave rise to them, and all the buds, the parent embryo included, later develop into medusæ. In *Cunina*, however, the parent embryo which gives rise to buds undergoes no further development, only the buds continuing on their course of growth to medusæ. In this case a true and typical alternation of generations occurs and points out a simple explanation of the alternation which is found in the Anthomedusæ and Leptomedusæ. In these the polyp colonies are the results of non-sexual reproduction of a larval medusa, and some only of the individuals so formed continue their development to medusæ.

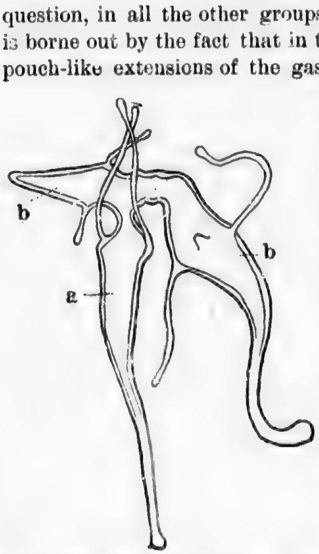

FIG. 49.—BUDDING LARVA OF *Cunoctantha octonaria* (after MCCREADY, from BROOKS).
a = egg larva.
bb = budded larvæ.

The relationships of the Hydrocorallinæ to the other groups are not yet quite demonstrated. It would seem, however, from the medusa-bud which occurs in one species of *Millepora* having its reproductive organs in the walls of the manubrium that the affinities of the group are with the Anthomedusæ, and that an exceptional amount of degeneration of the medusa had occurred in correspondence with the development of the calcareous corallum.

The Siphonophores are evidently allied to the Anthomedusæ, judging from the characters of their medusæ. The colony, however, contains both medusa and polyp individuals, the former not being in all cases reproductive as in the Anthomedusæ. The embryology of those members of the order which have been studied in this particular indicates that they too must be regarded as produced by budding in embryonic stages, some of the buds developing to medusæ, others remaining in the polyp stage. A further differentiation of the medusæ took place by which the pneumatophore, nectocalyces, and covering scales have been specialized from medusæ originally reproductive, the pneumatophore probably representing the parent individual of the colony. It is interesting to note in this connection that in some forms the reproductive medusæ after having expelled their ova or spermatozoa become converted into nectocalyces.

II. Class **Scyphomedusæ.**

In the Scyphomedusæ the medusa form is preëminent, the polyp form being placed in the background and occurring only as a larval stage, though in some forms it assumes somewhat greater importance on account of the power it may possess of reproduction by transverse division.

The medusæ are usually free-swimming, though a few of the more lowly organized forms are attached throughout their lives by a prolongation of the exumbrellar surface (Fig. 52), forming a connecting link between the free-swimming forms and the polyp. As a rule they reach a much greater size than do the Hydromedusæ, from which they are further distinguished by (*a*) the absence of a velum, (*b*) by the sense-organs when present being modified tentacles, and (*c*) by the reproductive cells always arising in the endoderm. On account of the first of these characters the Scyphomedusæ are sometimes termed the *Acraspeda*.

They are all more or less bell-shaped, a number of tentacles usually hanging from the margin of the bell (Fig. 53). These, however, are frequently secondarily developed, there being in the simpler forms eight primary tentacles which may persist as tentacles, or four or all of them may be converted into sense-organs (Fig. 50, *s*) situated near the margin of the bell and more or less enclosed in special chambers by the growth around them of folds of the bell substance (*l*). From the centre of the subumbrella there hangs the manubrium (*m*), the extremity of which is frequently prolonged into four elongated mouth-lobes, and above it communicates with the gastric cavity, *g*, which in simple forms extends to the margin of the bell, being obliterated only at four interradial points or lines. The four broad radial pouches thus produced correspond with the radiating canals of the craspedote medusæ, and the line of fusion being imperfect at the margin of the bell a communication between adjacent pouches is present comparable to the craspedote circular canal. This condition is, however, only retained in the simpler forms; in the higher Scyphomedusæ the lines or points of obliteration may be omitted, and by secondary obliterations taking place over various areas of the cœlenteron, and by its irregular extension towards the rim of the bell as this grows in diameter, a complicated branching arrangement of the peripheral portion of the cœlenteron is produced, in which, however, the original 4-radial arrangement is as a rule distinctly indicated. Along the interradial axes there are four deep depressions of the subumbrellar surface, the *funnels* or *subgenital chambers* (Fig. 50, *sg*), above which lie the horseshoe-shaped reproductive organs, *r*, developed in the cœlenteric endoderm, one limb of each horseshoe lying in each of the adjacent radial pouches.

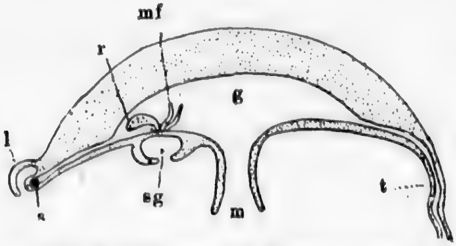

FIG. 50.—DIAGRAM OF SCYPHOMEDUSA.

g = gastric cavity.
l = lobe covering the sense-organ.
m = mouth.
mf = mesenterial filaments.
r = reproductive organs.
s = sense-organ.
sg = subgenital cavity.
t = tentacle.

Finally, in the line of each interradius there project into the cœlenteric cavity a number of coarse thread-like filaments, the *mesenterial filaments* (*mf*), which are unrepresented in the Hydromedusæ.

Such is the general structure of the Scyphomedusæ; the modifications will be better described in connection with the various orders into which the class may be divided. In histological structure the resemblance to the Hydromedusæ is so great as to do away with the necessity of a detailed account, except as regards the sense-organs. As already stated, these when present are modified tentacles and partake of the characters of both eyes and otocysts. They are usually short finger-like stalks, lying in a notch of the rim of the bell and covered over by folds (*covering plates*, Fig. 51, *cp*) arising from the adjacent substance of the bell on either side of the niche and frequently uniting so that the stalks lie in pouch-like cavities. The ectoderm of the finger-like stalks contains numerous sensory and ganglion cells, and at one or more regions pigment-cells are associated with these to form the eye (*o*), which may be further perfected by the addition of a cuticular lens. The stalks are hollow, containing a prolongation of the cœlenteric cavity (*cc*) lined by endoderm, and at the tip of the stalk the endoderm-cells are filled with crystals of carbonate of lime, the whole mass of crystals forming a rather large otocyst (*ot*). The covering plates, furthermore, above the sensory stalks are usually grooved, the bottom of the groove

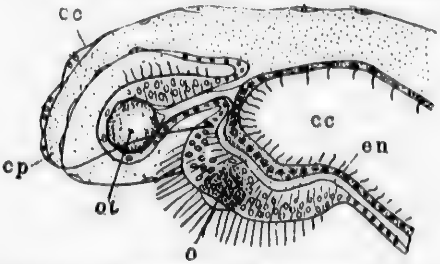

FIG. 51.—MARGINAL SENSE-ORGAN OF *Rhopalonema* (after HERTWIG).

cc = cœlenteric cavity.
cp = covering plate.
ec = ectoderm.
en = endoderm.
o = eye.
ot = otocyst.

being lined by sensory cells to which an olfactory function is attributed. The marginal sense-organs of the Scyphomedusæ are thus much more complicated in structure and in addition have a different mode of origin than those of the Hydromedusæ.

1. Order **Stauromedusæ**.

In this order some of the forms are fixed throughout their adult life, e.g. *Lucernaria* (Fig. 52); while others are free-swimming when mature, as *Tessera*. The deep bell has at the margin eight tentacles—the primary tentacles, none of which become modified into sense-organs, these structures being wanting in the group. In some species of *Lucernaria* these primary tentacles (*t*) are somewhat altered, and in all the margin of the bell is produced into eight knob-tipped lobes, to each of which a bunch of secondary tentacles may be attached. The cœlenteron extends out to the margin of the bell, and is interrupted along the interradii by a point

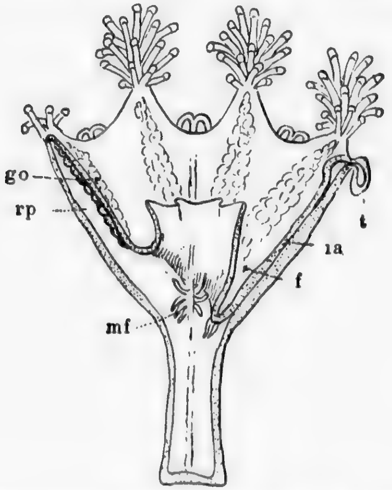

FIG. 52.—*Haliclystus auricula* DIVIDED LONGITUDINALLY (after H. JAMES-CLARK).

f = funnel.
go = reproductive organs.
ia = interradial adhesion.
mf = mesenterial filaments.
rp = radial pouch.
t = modified primary tentacle.

(*Tessera*) or line (*Lucernaria*) of adhesion. The depressions of the subumbrellar surface, the funnels (*f*), are very deep in *Lucernaria*, extending almost to the summit of the bell.

2. Order **Peromedusæ.**

In this order the adult medusæ are always free-swimming, and are characterized by the bell being pointed in shape and about its middle marked with a distinct constriction. The cœlenteron is obliterated at only four points, as in *Tessera*, and they differ from the Stauromedusæ by possessing four sense-organs, the four interradial tentacles of the primary series of eight becoming modified to form these structures, while the radial ones retain their original character.

3. Order **Cubomedusæ.**

This order, of which *Charybdea* (Fig. 53) is a typical example, is characterized by the bell being of a cubical shape. The interradial obliterations of the cœlenteron are linear, and, as in the preceding order, four of the primary tentacles, these being the only ones which develop, are modified to form sense-organs. In this order, however, it is the four radial tentacles which form the sense-organs (*so*), the four interradial persisting as tentacles (*t*).

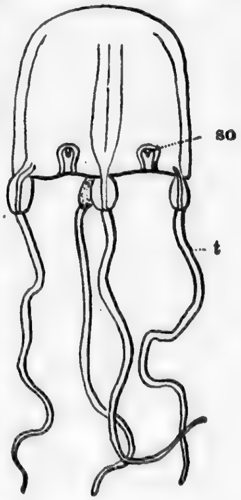

Fig. 53.—*Charybdea marsupialis* (after CLAUS).
so = sense-organ.
t = tentacle.

4. Order **Discomedusæ.**

In this order, which includes the majority of the known Scyphomedusæ, all the eight primary tentacles are converted into sense-organs, a number of secondary tentacles usually developing at the margin (Fig. 54). The primary interradial obliterations of the cœlenteron do not develop, but on the other hand secondary obliterations frequently make their appearance, which, combined with irregularities of growth of the cœlenteron, give its peripheral portions an irregular outline (*Cyanea*), or convert them into a series of anastomosing canals, e.g. *Aurelia*. The margin of the bell is usually more or less lobed, eight of these lobes being especially distinct and carrying the sense-organs, the intervals between them being usually occupied by the secondary tentacles when these are present. The depressions of the subumbrellar surface are no longer deep funnels, but form rather shallow *subgenital chambers* with thin roofs, into the cavity of which the reproductive organs bulge out.

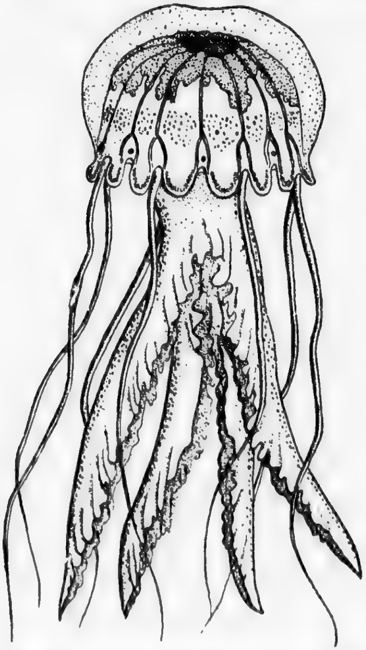

Fig. 54.—*Pelagia cyanella* (after Agassiz).

In many forms the margins of the mouth are prolonged into long fringed lobes, and in one family, the *Rhizostomidæ* (e.g. *Stomolophus*), the margins of these lobes may fuse together, leaving, however, a large number of minute openings along the line of fusion. These lead into canals traversing the substance of the lobes, and uniting finally in a larger central canal at the upper extremity of which lies the original mouth.

Development of the Scyphomedusæ.—The segmentation of the ovum leads as usual to a blastula form which may become solid by immigration and subsequently hollow out, or may abbreviate these processes by a typical invagination. The gastrula resulting passes in some forms gradually into the adult condition (*Pelagia*), without ever relinquishing its free-swimming habits, though in the majority of cases in which the life-history is known, cases confined entirely to the Discomedusæ, the embryo settles down and leads for a time a fixed sessile existence, resembling very much a polyp. This polyp form (Fig. 55, *A*), known as the *Scyphostoma*, differs materially from the hydroid polyp; in the first place, from the body-wall there project into the cœlenteron four linear ridges (mesenteries) which extend from the neighborhood of the mouth to the posterior end of the cœlenteron, and later give rise to the mesenterial filaments of the medusæ; and in the second place, a deep funnel-like depression extends into each one of these mesenteries from the oral surface of the Scyphostoma, and produce later the subgenital chambers of the medusæ.

The Scyphostoma may develop directly into the free-swimming medusæ, but in a number of forms it undergoes a series of transverse divisions (Fig. 55, *B*) into a number of saucer-like structures produced at the edges into eight blunt notched prolongations. These separate from the parent Scyphostoma and are known as *Ephyræ* (Fig. 55, *C*), developing into the adult Discomedusan by the intervals between the eight lobes, which carry the sense-organs, filling out, by the development of tentacles, and by the growth of the cœlenteron. A typical alternation of generations is thus brought about.

There can be little doubt but that the ancestral Scyphomedusan was a sessile organism with much resemblance to *Lucernaria*. From this two lines of descent arose, both marked by a development of sense-organs from tentacles and terminating in the Peromedusæ and Cubomedusæ respectively, the Discomedusæ resulting in the culmination of this sense-organ development. So far as the Discomedusæ themselves are concerned the

Ephyra seems to represent an ancestral stage, since some mature medusæ resemble this stage very closely and it occurs in the life-history of all, and earlier than this is the Scyphostoma representing the *Lucernaria* stage of evolution. The Scyphostoma has superficial resemblance to a hydroid polyp, which resemblance is almost an identity in the earlier stages of the Scyphostoma before the development of the mesenteries and funnels. This suggests a relationship of the Scyphomedusæ to the Hydromedusæ only through the polyp, the separation of the two classes having occurred before the appearance of the medusæ on the scene.

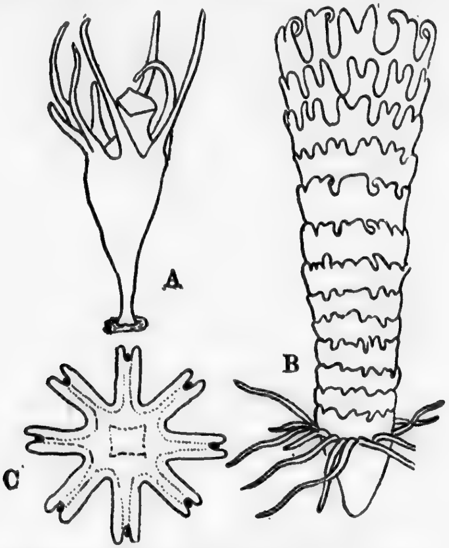

FIG. 55.—*A*, Scyphostom of *Aurelia*; *B*, Strobila of *Aurelia*; *C*, Ephyra of *Pelagia* (all after AGASSIZ).

III. CLASS **ANTHOZOA**.

The Anthozoa never assume the medusa form, but are sessile, usually colony-producing polyps of the Scyphostoma type. Typically they are cylindrical structures (Fig. 56) attached at one extremity, the *base*, and bearing at the other extremity the mouth in the centre of a flat surface, the *disk*, around the margins of which are a number of hollow tentacles. The cœlenteron is imperfectly divided into a number of chambers by longitudinal partitions arising from the body-wall, the *mesenteries* (Fig. 57, *me*), the various intermesenterial chambers communicating freely with a central space. The mouth does not open directly into the cœlenteron, as in the hydroid polyps, but into a tube, the *stomatodæum* (*st*), lined by ectoderm and communicating freely below with the central cœlenteric space. Certain of the mesenteries in their upper portions are attached to the endodermic surface of the stomatodæum, but below its lower end all have free edges. Along this free edge there runs, in most of the mesenteries, a cylindrical thickening, the *mesenterial filament*, composed in its lower portion of cnidoblasts and gland-cells, and usually longer than the mesentery, on the edge of which it forms a complicated system of coils and twists. In its lower part the filament in some forms separates from the mesentery as a bunch of fine filaments richly provided with nematocysts and capable of being protruded from the mouth or through pores in the body-wall. The upper part of the filament is usually of different structure, bearing on each side a band of elongated ciliated cells whose function it is to produce a circulation of the fluids in the cœlenteron.

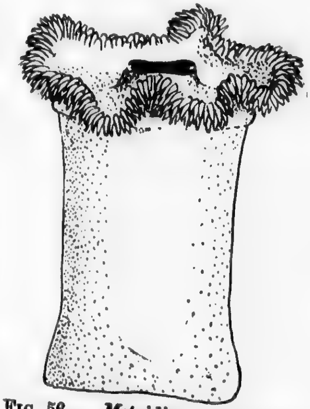

Fig. 56. — ***Metridium marginatum*, Les.**

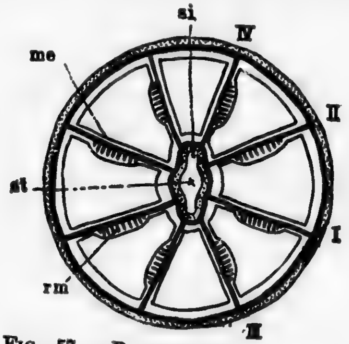

Fig. 57. — Diagrammatic Transverse Section through *Edwardsia* in Region of Stomatodæum.

me = mesentery.
rm = retractor muscle.
si = siphonoglyphe.
st = stomatodæum.
I–IV = mesenteries in the order of their development.

The reproductive cells develop in the [illegible]derm of the mesenteries, whence they are shed into the intermesenterial chamber and make their exit by the mouth. The nervous system is well developed especially in the ectoderm of the disk and tentacles, though it also occurs in the endoderm. It possesses the general character of the Cœlenterate nervous tissue consisting of sensory cells, nerve-fibres, and ganglion-cells. The muscular system is very well developed both in the ectoderm and endoderm, the muscle-fibres being generally longitudinal in the former layer, and in the latter circular in their direction. At certain regions of the body the muscle-fibres are especially abundantly developed, the mesoglœa being thrown into complicated folds for their support, so that it is possible to distinguish certain definite muscles. One of these is developed upon one face of each mesentery, and, its fibres being directed longitudinally, it forms a strong *retractor* (Fig. 57, *rm*) for the disk and tentacles; a second is developed in the endoderm of the body-wall a short distance below its junction with the disk, and its fibres may, by the growth of the mesoglœa around them, become imbedded in that layer; it forms a more or less powerful *sphincter*, serving to cover in the disk and tentacles when these have been retracted by the mesenterial retractors.

The Anthozoa are constructed upon a radial symmetry, as are the other Cœlentera, this symmetry appearing in the arrangement of the mesenteries and tentacles and in the cylindrical form of the body. Nevertheless it is always possible to divide the Anthozoan by a single plane into two similar halves, that is, a bilateral symmetry is also present which is produced by the arrangement of the retractor muscles on only one face of each mesentery and by the flattening of the stomatodæum. This latter feature is furthermore usually made more pronounced by the occurrence, at one or both ends of the longer transverse axis of the stomatodæum, of a distinct groove lined by high columnar cells with long cilia, these grooves forming the *siphonoglyphes* (Fig. 57, *si*), and by the mesenteries which are attached to the stomatodæum in the neighborhood of the siphonoglyphes usually having their retractor muscles on different faces from those on which they occur in the other mesenteries.

Frequently the ectoderm of the anthozoan polyps secretes a skeletal substance which may either be carbonate of lime, or else an organic substance of a horny consistency. In the corals the secretion takes the form of carbonate of lime and forms a cup (Fig. 58, *ap*) in which the polyp is seated, ridges

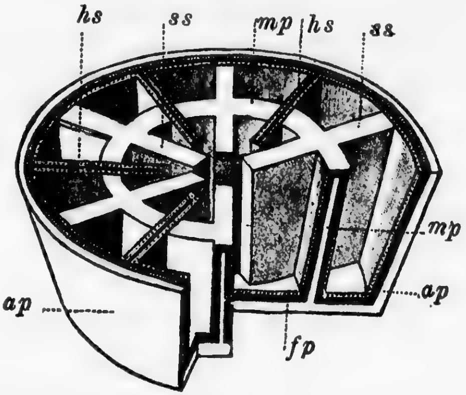

FIG. 58.—DIAGRAM OF THE STRUCTURE OF A CORAL (after VON KOCH, from LANG).

ap = exotheca.
fp = basal plate.
hs = mesentery.
ss = septa.

Calcareous skeleton, white; ectoderm, shaded; mesoglœa, black; endoderm, dotted.

(*septa*, *ss*), over which the soft tissues of the animal are moulded, projecting up from the bottom of the cup. The septa may be united by delicate tangential bars, *synapticulæ*, and from the bottom of the cup a somewhat cylindrical *columella* may project, other upright rods, the *pali*, intervening between the free edges of the septa and the columella. The upper portion of the body-wall of the polyp is reflected over the rim of the calcareous cup and may produce ridges, *costæ*, on its outer surface corresponding in position with the septa, and inasmuch as the cup is continually increasing in depth so long as the polyp lives, and the polyp only occupies the upper portion, the lower part may from time to time be separated off by a transverse partition or *dissepiment*.

In other forms, such as the Alcyonarians, however, the skeleton is secreted only by the basal ectoderm and the colony becomes moulded over it (Fig. 59), so that it forms a central horny or more or less calcified axial support, and in addition the mesoglœal cells secrete scattered particles of carbonate of lime, having a more or less definite form for each species, but not uniting together to form a firm skeleton.

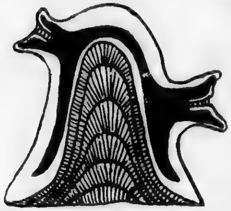
FIG. 59.—DIAGRAM OF YOUNG GORGONIAN (after VON KOCH).

The development of the Anthozoa is always direct, and the diploblastic condition is produced by delamination of the cells of the blastula. Many adult forms possess the power of division, either transverse or longitudinal, the latter giving rise to complex colonies in many cases. In other forms the primary polyp may develop a stolon from which other individuals may bud, producing a diffuse colony, or the intervals between the individuals may be filled up by a growth of mesoglœa traversed by a network of canals, forming a tissue, the *cœnenchyme* (Fig. 60), in which the various individuals are imbedded.

The class Anthozoa may be divided into a number of orders, whose existence depends mainly on the arrangement of the mesenteries.

1. Order **Alcyonariæ.**

The majority of the Alcyonarians produce colonies by budding. In some the individuals are scattered on stolons, in others imbedded in a cœnenchyme (*Alcyonium*, Fig. 60), or in others united to form fleshy colonies of a feather or reniform shape (*Renilla*), the whole being imbedded in the sand on a fleshy stalk. In some of the groups a horny or calcareous skeleton is present in addition to the calcareous spicules imbedded in the mesoglœa and may form a central axis enclosed by the cœnenchyme (Fig. 59) and of a horny consistency, as in *Gorgonia* and *Leptogorgia*, or more or less calcareous, as in *Isis* and *Corallium*, the skeleton of the latter constituting the red coral of commerce. In the Organ-pipe Coral, *Tubipora*, each individual lives in a calcareous tube, the various tubes being united by transverse plates, and in *Heliopora* the skeleton becomes very massive, resembling that of the ordinary corals even to the occurrence of septa projecting into the interior of the cups which contain the individual polyps.

Notwithstanding these manifold variations of the skeleton and of the colony form, the individual polyps present throughout a great similarity of structure. They possess only eight pinnate tentacles and eight mesenteries whose retractor muscles are arranged in the manner shown in the annexed diagrammatic cross-section of a polyp (Fig. 61). In *Renilla* and allied forms, such as *Pennatula*, a slight polymorphism occurs, certain polyps possessing no tentacles and functioning as *inhalent zooids* through which currents of water pass into the cœlenteric cavities of the colony through which they circulate.

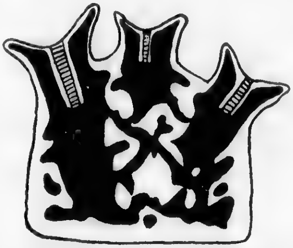

Fig. 60.—Diagram of Young Colony of *Alcyonium* (after von Koch.

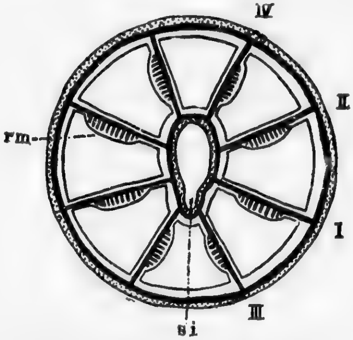

Fig. 61.—Diagrammatic Transverse Section of an Alcyonarian.
rm = retractor muscle.
si = siphonoglyphe.
I–IV = mesenteries.

2. Order **Edwardsiæ.**

The Edwardsiæ never produce colonies nor do they possess a skeleton, though frequently the exterior of the body is encrusted by foreign particles. They live usually imbedded in sand, the base being rounded and not adhesive, and possess eight (sometimes sixteen or thirty-two) simple tentacles and eight mesenteries, differing from those of the Alcyonarians in the arrangement of the retractor muscles as shown in Figure 57.

3. Order **Ceriantheæ.**

The Ceriantheæ are, like the Edwardsiæ, solitary forms destitute of a skeleton, and live imbedded in sand or mud. The basal region is rounded and not adhesive, having at the centre a pore which communicates with the cœlenteron. In *Cerianthus* a fibrous investment surrounds the body as a tube, secreted by the ectoderm, this layer of the body being further characterized by an enormous development of muscle-fibres arranged longitudinally and supported upon slender processes of the mesoglœa of the body-wall. The tentacles are simple and very numerous, being arranged in two sets, one surrounding the margin of the funnel-shaped disk and the other immediately surrounding the mouth. The mesenteries are also very numerous and are distinguished by the absence in the adult of retractor muscles, the ectodermal muscles playing the part of the retractors, and the characteristic Anthozoan sphincter is also absent. The arrangement of the mesenteries (Fig. 62) is peculiar to the group, new ones continuing to form during the entire life of the animal and making their appearance one on each side of the sagittal plane between the two which immediately preceded them. The older mesenteries are thus crowded to one surface of the body, the dorsal surface, at which the single siphonoglyphe (*si*) occurs in the stomatodæum, and the four on either side of the mid-dorsal line (*I–IV*) are the homologues of the eight mesenteries of the Edwardsiæ, the rest being secondary structures not represented in that group.

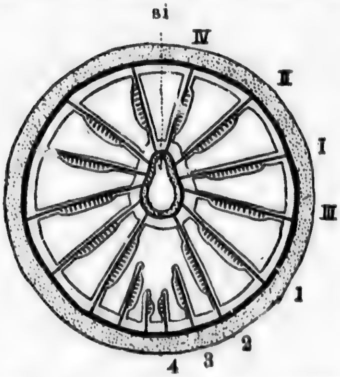

FIG. 62.—DIAGRAMMATIC TRANSVERSE SECTION OF A YOUNG *Cerianthus* (according to CARLGREN).
si = siphonoglyphe.
I-IV = the Edwardsian mesenteries.
1-4 = secondary mesenteries.

4. Order **Antipathariæ.**

The members of this order are all colonial and secrete a branching axial skeleton of a black horny material. The polyps possess usually but six simple tentacles, and as a rule only six mesenteries are present, of which only the two lying in the transverse axis bear reproductive organs and mesenterial filaments; in some forms four or six additional imperfectly-developed mesenteries are present, but six seems to be the number typical for the group.

5. Order **Protactiniæ.**

This order includes a group of forms, all simple and with simple tentacles, but showing considerable variation in the number of the tentacles. They all agree in this particular, however, that there are twelve mesenteries arranged in pairs (Fig. 63, *I–VI*), the two pairs attached to the siphonoglyphe region of the stomatodæum having their retractor muscles on the faces turned away from each other, while in the other four pairs they are on adjacent faces. The two former pairs are termed the *directive mesenteries* (Fig. 63, *D* and *D'*), their constituent mesenteries lying one on each side of the sagittal plane, and together with one mesentery (*II* and *I*) from each of the other pairs represent the eight Edwardsian mesenteries. To these six primary pairs a varying number is added in the different forms; it may be, on each side, one between one of the pairs of directives and the adjacent lateral pair (*Scytophorus*), or a pair in the same locality (*Gonactinia*, Fig. 63, 7), or two pairs one of which corresponds to the pair of *Gonactinia*, the second pair lying between the two lateral primary pairs (*Oractis*).

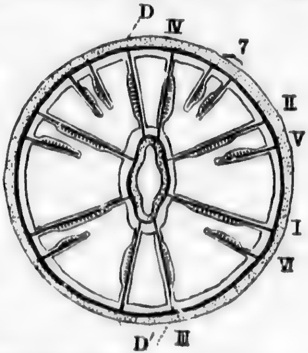

Fig. 63.—Diagrammatic Transverse Section of *Gonactinia*.

D, D' = directive mesenteries.
I–IV = the Edwardsian mesenteries.
V, VI = mesenteries forming pairs with *II* and *I*.
7 = secondary pair of mesenteries.

In all these forms there is a strictly bilateral arrangement of the mesenteries, and a tendency for them to arrange themselves in pairs.

6. Order **Zoantheæ.**

The Zoantheæ form very frequently colonial aggregates either of a diffuse stoloniferous character (*Zoanthus*) or of a more compact form, the individuals being imbedded in a cœnenchyme (*Palythoa*). No skeleton is present, though many forms have a dense crust on the outside of the body formed of particles of sand, sponge-spicules, radiolarian and foraminiferan shells, etc., imbedded in the outer portion of the mesoglœa. They possess a varying number of simple tentacles, and there is only a single siphonoglyphe which marks the ventral surface of the body. The mesenteries are arranged in pairs, six of which (Fig. 64, *I–V*, *II–VI*, *III* and *IV*) correspond with the six primary pairs of the Protactiniæ; of these the dorsal directives (*D*) are never united to the stomatodæum and the dorsal lateral pair (*II*, *VI*) consists of one perfect and one imperfect mesentery, the latter being ventral to the former. The ventral lateral primary pair may consist of two perfect mesenteries or may have the same arrangement as the dorsal lateral pair. To these six pairs a varying number of secondary pairs (1–4) may be added, the new pair always arising immediately on either side of the ventral directives. Each of the new pairs consists of a perfect and an imperfect mesentery, the latter being the dorsal one of the two, these secondary pairs thus differing from the lateral primary mesenteries.

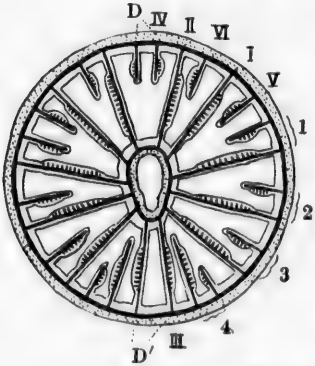

FIG. 64.—DIAGRAMMATIC TRANSVERSE SECTION OF *Zoanthus*.
D, *D′* = directive mesenteries.
I–VI as in preceding figure.
1–4 = pairs of secondary mesenteries.

7. Order **Hexactiniæ**.

In the Hexactiniæ the six primary pairs of mesenteries described as occurring in the two preceding orders are again found (Fig. 65, *I*, *D*, and *D*), and in a few forms (*Halcampa*) may be the only ones present. As a rule, however, a varying number of secondary pairs develop, each of these appearing in the interval between two primary pairs, so that two cycles of mesenteries (*I* and *II*) may be distinguished. Usually, however, the process of mesentery formation does not stop here, tertiary (*III*), quaternary, etc., cycles being developed, the pairs of each new cycle appearing in the intervals between the pairs of the cycles already present. Consequently, since there are six primary pairs, the second cycle will consist also of six pairs, the third of twelve, the fourth of twenty-four, and so on. In a few forms, owing to the precocious development of one or two of the secondary pairs on each side, the symmetry becomes converted from an hexamerous one to an octamerous (*Aiptasia annulata*) or a decamerous one (*Tealia*).

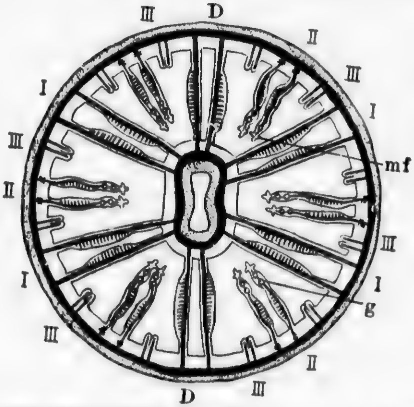

FIG. 65.—DIAGRAMMATIC TRANSVERSE SECTION OF AN HEXACTINIAN, *Aiptasia*, with only the mesenteries of the first cycle perfect.

D = directive mesenteries.
g = reproductive region of mesentery.
mf = mesenterial filament.
I = mesenteries of the first cycle.
II = " " " second "
III = " " " third "

Since the tentacles develop in connection with the spaces between the mesenteries, they are arranged in cycles corresponding to the mesenteries. Usually but a single tentacle communicates with each space, but in some forms a series may arise on the roof of each space so that the tentacles have a radiating arrangement (*Discosoma*) or may appear to be irregularly scattered, as in some corals (*Fungia*). They are usually simple in form, though they may be in some cases pinnate (*Phymanthus*, *Thalassianthus*) or even branched.

The order is usually divided into two suborders:

1. Suborder *Malacodermata*.

This includes the Sea-anemones or Actinians, all simple forms, not producing colonies, and usually attached by an adhesive base. They never form a skeleton of any kind, though they may develop an enveloping cuticle, usually very thin and in some cases encrusted with foreign matter; this is more especially the case with deep-water forms, the shallow-water forms, such as *Metridium*, *Bunodes*, etc., lacking a cuticle. Many forms possess the power of division, the individuals so produced separating completely and not forming colonies; furthermore some forms reproduce non-sexually by separating off portions of the tissue at the margin of the base, each portion eventually developing into an adult Actinian.

2. Suborder *Sclerodermata*.

This suborder includes the ordinary corals, which secrete a calcareous skeleton of the character already described (p. 107). A few forms are simple, but the majority produce complex colonies by longitudinal division and by budding, while in others the division is only carried to the extent of the formation of an individual with a number of mouths, as in *Fungia* and *Manicina*. In most of the forms the corallum is tolerably dense and may be either branching, as in *Oculina*, or form massive blocks, as the Brain-stone Coral (*Mæandrina*), but in *Madrepora* it is more or less porous.

The Corals are most abundant in tropical seas and in shallower water, the Madrepores forming under such conditions large reefs, in the lagoons of which the Fungias, Manicinas, and Mæandrinas are found. In colder seas but few forms (*Astrangia*) are found in shallow water, but in the greater depths of the ocean the simple forms which do not produce colonies are frequently found.

Relationships of the Anthozoa.—As has been pointed out, it seems probable that the Anthozoa are to be traced back to a Scyphostoma-like polyp lacking interradial funnels. No four-mesenteried form, however, is known, a large gap existing between the Scyphostoma and the Alcyonaria, which are probably the simplest Anthozoa known to us. The primitive Alcyonaria were undoubtedly simple forms, and from them to the Edwardsiæ was not a very great step. By the formation of four additional mesenteries the Edwardsian condition became converted into the twelve-mesenteried condition which forms the ground-form of the Protactiniæ, Zoantheæ, and Hexactiniæ, the various stages seen in the Protactiniæ indicating the manner in which the Hexactinian condition has been brought about. The Ceriantheæ seem to be offsets from the Edwardsian condition, but it is difficult in the present state of our knowledge to conjecture the affinities of the Antipatharia.

It is noticeable that the members of all the orders except the Hexactiniæ have a strictly bilateral arrangement and development of the mesenteries; this arrangement becomes gradually modified, first, by the tendency of the mesenteries to arrange themselves in pairs; second, by the formation of secondary mesenteries; third, by a tendency for these to appear in pairs; fourth, by a tendency for such pairs to appear in all the intervals between the primary pairs. Thus the Anthozoa are forms which are gradually specializing away from the radial symmetry characteristic of all Cœlenterates towards a bilateral symmetry, and the more pronounced radiality of the Hexactiniæ is a secondary condition.

SUBKINGDOM METAZOA.

TYPE CŒLENTERA.

I. Subtype PORIFERA.—With pores in the walls and without nematocysts.
  1. Order *Calcarea.*—Skeleton calcareous.
    (*a*) Ascon type. ***Leucosolenia.***
    (*b*) Sycon type. ***Grantia.***
  2. Order *Cornacuspongiæ.*—Skeleton of spongiolin, usually with simple siliceous spicules.
    (*a*) With spicules; fresh water. ***Spongilla, Ephydatia.***
    (*b*) Without spicules; marine. ***Euspongia.***
  3. Order *Spiculispongiæ.*—Skeleton of uniaxial or tetraxial siliceous spicules. Sometimes entirely wanting.
    (*a*) Skeleton wanting. ***Halisarca.***
    (*b*) Skeleton present. ***Cliona, Esperella.***
  4. Order *Hyalospongiæ.*—Skeleton of 6-rayed siliceous spicules. ***Euplectella.***

II. Subtype CNIDARIA. Without pores in walls and with nematocysts.

I. Class HYDROMEDUSÆ.—Ectoderm and endoderm meet at mouth. Reproductive organs develop in ectoderm. Medusa with velum; sense-organs not modified tentacles.

1. Order *Hydrariæ.*—No medusa form; tentacles hollow. *Hydra.*
2. Order *Narcomedusæ.*—No hydroid form; sense-organs otocysts of endodermal origin; radiating canals represented by broad pouches. *Cunoctantha, Cunina.*
3. Order *Trachymedusæ.*—No hydroid form; sense-organs otocysts of endodermal origin; radiating canals narrow. *Liriope, Geryonia, Rhopalonema.*
4. Order *Leptomedusæ* or *Campanulariæ.*—With both hydroid and medusoid forms, the latter frequently degenerate. Hydranths with hydrothecæ; gonangia present. Medusa with otocysts of ectodermal origin; reproductive organs on radial canals.
    (*a*) Hydroid and medusoid forms both well developed. *Eucope, Obelia.*
    (*b*) Hydroid form not well developed. *Æquorea, Rhegmatodes.*
    (*c*) Medusoid form degenerate. *Sertularia, Halecium, Aglaophenia.*
5. Order *Anthomedusæ* or *Tubulariæ.* With both hydroid and medusoid forms, the latter frequently degenerate. Hydroid forms without hydrothecæ or gonangia. Medusoid forms with eye-spots; reproductive organs developed in wall of manubrium.
    (*a*) Medusoid form well developed. *Margelis, Coryne, Pennaria.*
    (*b*) Medusoid form degenerate. *Clava, Hydractinia, Tubularia, Eudendrium.*
6. Order *Hydrocorallinæ.*—Hydroid forms polymorphic; secreting calcareous skeleton by ectoderm. Medusoid forms usually degenerate. *Millepora, Stylaster.*
7. Order *Siphonophora.*—Free-swimming, pelagic, polymorphic colonies.
    (*a*) Nectocalyces present, without pneumatophore. *Diphyes.*
    (*b*) With both nectocalyces and pneumatophore. *Agalma.*
    (*c*) With pneumatophore only. *Caravella.*
    (*d*) Discoidal forms without nectocalyces. *Velella, Porpita.*

II. Class SCYPHOMEDUSÆ.—With medusoid form only in adult stage. Velum not present; sense-organs are modified tentacles. Reproductive organs develop in endoderm.

1. Order *Stauromedusæ.*—With the eight primary tentacles not at all or but slightly modified. *Tessera, Lucernaria.*
2. Order *Peromedusæ.*—With the four interradial primary tentacles transformed into sense-organs.

3. Order *Cubomedusæ.*—With the four radial primary tentacles transformed into sense-organs. *Charybdea.*
4. Order *Discomedusæ.*—With all eight primary tentacles transformed into sense-organs.
   (*a*) Mouth-lobes not fused. *Cyanea, Aurelia, Pelagia.*
   (*b*) With mouth-lobes fused. *Stomolophus.*

III. Class ANTHOZOA.—Without medusoid forms. With ectodermal stomatodœum; cœlenteron divided into chambers by vertical mesenteries; reproductive organs developed in the endoderm.

1. Order *Alcyonaria.*—Colonial forms with eight mesenteries not arranged in pairs; tentacles pinnate.
   (*a*) Without axial skeleton. *Renilla, Alcyonium, Pennatula.*
   (*b*) With axial skeleton. *Gorgonia, Leptogorgia, Isis, Corallium.*
   (*c*) With tubular calcareous skeleton. *Tubipora.*
2. Order *Edwardsiæ.*—Simple forms with eight mesenteries not arranged in pairs; tentacles simple. *Edwardsia.*
3. Order *Ceriantheæ.*—Simple forms with numerous mesenteries not arranged in pairs; new mesenteries formed on each side of dorsal mid-line. *Cerianthus.*
4. Order *Antipathariæ.*—Colonial forms with axial horny support; with six simple tentacles; mesenteries not arranged in pairs. *Antipatharia.*
5. Order *Protactiniæ.*—Simple forms with twelve primary mesenteries arranged in pairs, and in addition one unpaired mesentery on each side, or one or two pairs. *Scytophorus, Gonactinia, Oractis.*
6. Order *Zoantheæ.*—Simple or colonial forms with twelve primary mesenteries arranged in pairs, and in addition a varying number of secondary pairs developed on each side of the primary pair occupying the mid-ventral line. *Zoanthus, Palythoa.*
7. Order *Hexactiniæ.*—Simple or colonial forms with twelve primary mesenteries arranged in pairs, and in addition a variable number of secondary pairs arranged in cycles, the newer pairs developing in the intervals between the pairs already present. An external calcareous skeleton present in many forms.
   (*a*) Without calcareous skeleton (*Malacodermata*). *Halcampa, Aiptasia, Tealia, Metridium, Bunodes.*
   (*b*) With a calcareous skeleton (*Sclerodermata*). *Madrepora, Fungia, Manicina, Mæandrina, Astrangia.*

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CHAPTER VI.

THE CTENOPHORA.

The group of forms known as the Ctenophora, to which the systematic value of a class may be given, present no little general resemblance to the Cœlentera, but at the same time depart so widely in structural and histological characters from the Cnidaria and Porifera that it seems advisable, until further evidence is forthcoming, to consider them as a group apart.

All the Ctenophores are pelagic and are of great transparency and delicacy, due to the nature of the mesoglœal tissue.

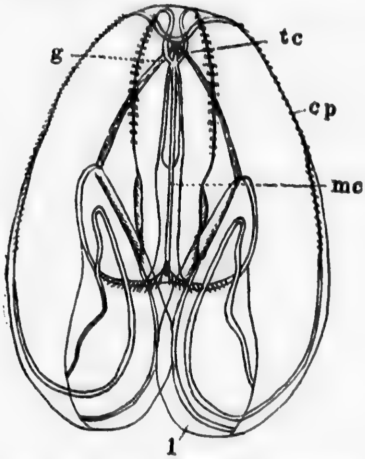

Fig. 66.—*Bolina hydatina* (after Chun).

cp = ciliated plates.
g = stomach or funnel.
tc = funnel-canal.
mc = stomodæal canal.
l = lobe.

In form they vary greatly, some being almost spherical or pyriform (*Pleurobrachia*), sometimes with broad lobes projecting from near the oral extremity (Fig. 66, *l*) (*Bolina*, *Mnemi-*

opsis), others being ribbon-like, as *Cestum*, the Venus' girdle, others sac-like, as *Beroë* and *Idyia*. Indications of a radial symmetry are seen in the eight longitudinal bands of cilia-plates (*cp*) which serve as locomotor organs, but this is thrown into the background by the more pronounced bilaterality. The stomodæum is flattened in one plane and the gastric cavity (*g*) in a plane at right angles to this, two tentacles, one on each side of the body, lying also in this plane. It is possible accordingly to recognize a sagittal plane, that of the stomodæum, and a transverse plane, that of the gastric cavity, and corresponding axes.

The mouth lies at the extremity of the vertical axis which is directed backwards in locomotion, and opens into the ectodermal stomodæum, which is flattened parallel to the sagittal plane. At its upper end the stomodæum opens into the endodermal gastric cavity (*g*) or so-called "funnel," from which five canals arise; one of these (*tc*) passes directly upwards to the aboral surface, where it branches and opens to the exterior by usually two openings; two others pass downwards parallel with the broad surface of the stomodæum (*mc*) and end blindly; while the other two (Fig. 67, *rc*) pass directly outwards in the transverse axis of the body and end at the base of the tentacles, a short distance before their termination giving off two branches, one on each side. These branches soon divide and give rise each to two canals which communicate peripherally with canals running longitudinally below the rows of *cilia-plates*.

These plates, which constitute the locomotor organs, are arranged one above the other and are composed of fused cilia arising from ectodermal thickenings. There are eight meridional rows of these ciliated plates, and from the upper end of each row a delicate groove lined with ciliated cells extends towards the aboral pole, each groove uniting with an adjacent one as they approach the pole, so that their number is reduced to four (Fig. 67, *cg*). These pass in upon the floor of a dome-shaped cavity enclosed by fused cilia which arch together at the centre but do not quite meet. The cavity thus enclosed is somewhat broader in the sagittal than in the transverse axis and contains the aboral sense-organ. The floor of the cavity is formed of high ciliated cells probably nervous in function, and above them is a mass of otoliths supported on four incurved rods of fused cilia, one of which forms the termination of each of the four meridional grooves.

In addition to this sense-organ, which is to be regarded as of the same function as the otocysts of the medusæ, there lies at each end of the sagittal axis of the sensory dome a so-called *pole-area* (Fig. 67, *p*), the cells of which are furnished with small plates of fused cilia, each area being surrounded by a thickened ciliated rim. These structures are from their form and situation supposed to be sensory, and an olfactory function has been attributed to them.

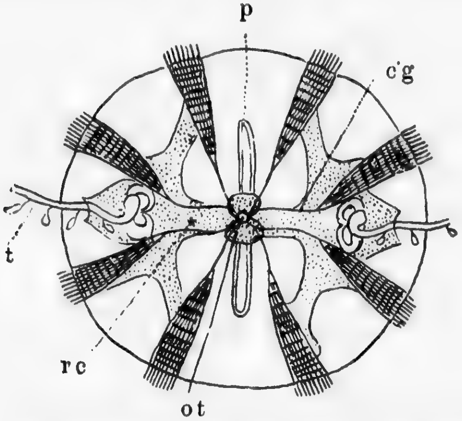

FIG. 67.—*Pleurobrachia* SEEN FOR THE ABORAL POLE (after AGASSIZ).

cg = ciliated groove.
p = polar area.
ot = otocyst.
rc = radial canal.
t = tentacle.

The tentacles (Fig. 67, *t*), of which there are two, situated at the extremities of the transverse axis, are present in all forms except the Beroids. Each tentacle lies in a deep depression termed the *tentacle-sheath* and consists of a principal axis which gives rise to a large number of secondary tentacles arranged upon one side only. Both the primary axis and the secondary tentacles are solid, being composed mainly of muscle-cells and containing no prolongation of the tentacular vessel. In *Mnemiopsis* and its allies and in *Cestum* the primary axis is practically wanting, the secondary tentacles arising directly from the bottom of the tentacle-sheath. The ectoderm of the secondary tentacles contains numerous cells supposed to be sensory, and also so-called *adhesive cells*, which in this group replace the nematocysts. They consist of a slender spirally-coiled muscular fibre (Fig. 68, *m*) attached at one extremity to the subjacent tissue and terminating at the other on the under surface of a hemispherical cap (*c*), whose surface is covered by small spherical masses of a sticky secretion. A small animal coming into contact with these caps is held by the adhesive secretion, the muscle-fibre being sufficiently elastic to yield to the struggles of the victim and to bring it in contact with the general ectoderm by contracting when its struggles cease.

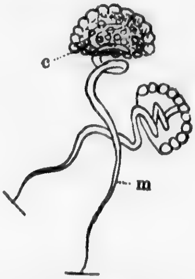

FIG. 68.—ADHESIVE CELLS FROM TENTACLE OF A CTENOPHORE (after CHUN).
c = adhesive cap.
m = contractile stalk

The reproductive organs lie in the outer walls of the canals which lie beneath the meridional rows of plates, but apparently are originally derived from the ectoderm. All the Ctenophores are hermaphrodites, the ova being arranged on one side of each canal and the spermatozoa on the other, in such a manner that the adjacent sides of any two canals bear the same kind of sexual cells. A peculiar phenomenon termed *Dissogony* has been observed in certain forms, consisting of the occurrence of two periods of sexual maturity in the life-history of the individual, the reproductive organs ripening first while it is still in a larval stage and again when it has reached its adult form.

The main bulk of the body of a Ctenophore is made up by a gelatinous tissue intervening between the endoderm and ectoderm and which may be termed the mesoglœa, though it is not improbable that its cellular elements are in great part derived from embryonic cells corresponding to the mesoderm-cells of higher forms. It consists of a gelatinous matrix through which are scattered branched cells and fibres. Some of the latter extend throughout the entire thickness of the mesoglœa and are inserted by their branched extremities into the ectoderm on the one side and the endoderm or stomodæal ectoderm on the other. They are contractile in function, consisting of a central protoplasmic axis containing a nucleus and of a peripheral contractile substance. In addition to these there are other much finer fibres which have been supposed to be nervous, and on the outer surface of the mesoglœa, between it and the bases of the ectoderm-cells, is a network of stellate ganglion-cells whose processes overlap but do not unite with each other. They are especially abundant in the region of the meridional rows of plates; just as the slender fibres of the mesoglœa are especially abundant below the aboral sense-organ and the meridional grooves, regions which recent observations have shown to be especially sensitive to stimuli.

The class may be divided into two orders:

1. Order **Tentaculata.**

The members of this order possess tentacles either with or without the primary axis. The simple forms, such as *Pleurobrachia*, belong to this order, as well as the lobate and ribbon-shaped forms. In the lobate forms, such as *Bolina* (Fig. 66) and *Mnemiopsis*, there is at each end of the sagittal axis a large lobe developed into which four of the meridional canals are continued; two of the canals, those nearest the extremities of the transverse axis, pass around the edge of the lobe and unite with each other, while the other two, which also unite, are thrown into arabesque-like twistings. The Venus'-girdle, *Cestum*, is ribbon-shaped, being flattened in the transverse plane and much drawn out in the sagittal plane; the result being the great extension of four of the meridional plate-rows and the almost complete disappearance of the other four. In its young stages, however, *Cestum* is a spherical form closely resembling the simple genus *Mertensia*.

2. Order **Eurystomeæ.**

This order, which includes the Beroid forms, is characterized by the entire absence of tentacles and by the wide bell-like stomodæum. The meridional canals send off along their course numerous branching processes into the mesoglœa and are united around the mouth by a circular canal. To this order belongs the Mediterranean genus *Beroë*, and the genus *Idyia* of the northwest Atlantic.

Relationships of the Ctenophora.—The Ctenophores have been by most authors assigned to the type Cœlentera, on account of their jelly-like consistency and the presence of gastro-vascular canals, and of indications of a radiate symmetry. It is possible, however, that these characters are simply superficial, and that the group possesses but very remote affinities to the Cœlenterates. They have furthermore been regarded by some as connecting links between the Cœlenterates and the Turbellarians, and in connection with this idea two aberrant forms may be briefly described. One, *Ctenoplana*, is a flattened form, on the middle of whose dorsal surface lies the otolith sac, and at a short distance from this are eight short rows of cilia-plates, each in a slight depression. Two tentacles lie in the transverse axis, and the mouth is situated at the centre of the lower surface and leads into a cavity from which numerous branching gastric pouches arise without any definite arrangement. The other form, *Cœloplana*, is also flattened and creeping ; the mouth lies on the under surface and opens into a wide cavity, which, as in *Ctenoplana*, gives origin to a number of pouches which branch and give rise to a network towards the periphery of the body ; a canal passes from the gastric cavity towards the dorsal surface of the body, where it divides into two branches which end blindly, and lying between them is a vesicle containing otoliths ; two tentacles similar to those of *Pleurobrachia* lie in the transverse axis. In both these forms the general surface of the body is ciliated, and they seem to represent intermediate forms between the Ctenophores and Turbellaria, *Ctenoplana* being more closely allied to the former and *Cœloplana* to the latter.

There are various important structural differences, however, between the Cœlentera and the Ctenophores. Among these may be mentioned the structure and position of the sense-organ, the structure and position of the mesoglœal muscle-fibres, the structure of the tentacles, the presence of the adhesive cells which cannot possibly be homologized with nematocyst-cells, and finally the early differentiation in the embryo of cells, resembling the mesoderm-cells of triploblastic animals, which give rise to the muscles of the tentacles and perhaps to some of the mesoglœal elements.

It seems not improbable that the affinities of the Ctenophores would be more accurately indicated in the classification if they were entirely removed from the Cœlentera and associated with the Turbellaria, being regarded as highly modified forms, adapted for pelagic life, descended from Turbellarian ancestors. The evidence which has been brought forward in favor of a relationship of the Turbellaria to the Cœlentera through the Ctenophores would support this view as well as that it was intended to support, and to this may be added the fact that while the peculiar adhesive cells of the Ctenophores cannot be homologized with any of the histological elements of the Cnidaria, they may readily have been evolved from the adhesive cells which occur in the ectoderm of many Turbellarians.

SUBKINGDOM METAZOA.

Class CTENOPHORA.—Pelagic organisms provided with eight meridional rows of plates formed by the fusion of cilia.

1. Order *Tentaculata.*—Ctenophora provided with tentacles.
    (*a*) Without lobes; more or less oval in shape. *Pleurobrachia*, *Mertensia.*
    (*b*) Lateral lobes occurring at oral pole. *Bolina*, *Mnemiopsis.*
    (*c*) Ribbon-like form. *Cestum.*
2. Order *Eurystomeæ.*—Without tentacles; stomodæum wide and bell-like. *Beroë*, *Idyia.*

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CHAPTER VII.

TYPE PLATYHELMINTHES.

THE Platyhelminths constitute a group which, though presenting a much higher grade of organization than the Cœlentera, nevertheless show certain general structural similarities to the representatives of that type. Thus upon the exterior of the body there is a thin ectoderm (Fig. 69, *D*, *ec*), below which is a *basement-membrane* (*bm*) sometimes thin, structureless, and destitute of cells, sometimes thicker and enclosing branched cells, and strictly comparable to the mesoglœa of the Cœlenterates. Within the basement-membrane there is a compact mass of tissue surrounding, in the

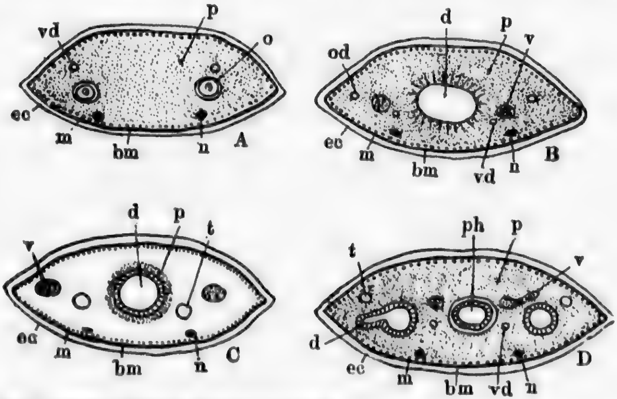

FIG. 69.—DIAGRAMMATIC TRANSVERSE SECTIONS THROUGH VARIOUS TURBELLARIA. *A*, an Acœlan; *B*, an Alloiocœlan; *C*, a Rhabdocœlan; *D*, a Triclad.

bm = basement-membrane.
d = intestine.
ec = ectoderm.
m = muscle-layer.
n = nerve.
o = ovary.
od = oviduct.
p = parenchyme
t = testis.
v = vitellarium.
vd = vas deferens.

majority of forms, a cavity, the enteron (*d*), the cells lining the walls of this being differentiated into a digestive epithelium or endoderm. The space between the enteron and the basement-membrane is occupied by the mesoderm, consisting peripherally of compact layers of circular and longitudinal muscle-fibres (*m*), while below these it forms a mass of nucleated cells, usually vacuolated so as to resemble a network of fibres enclosing spaces and constituting the *parenchyma* (*p*). It is traversed by dorso-ventral muscle-fibres and has imbedded in it various organs most of which are further differentiations of this middle germ-layer. These two layers, the endoderm and mesoderm, are together comparable with the inner layer of the Cœlenterates, the mes-endoderm, and when the enteron exists it communicates with the exterior, as in that group, by a single opening, the mouth, the Nemerteans only, the most highly organized class of the Platyhelminths, possessing a second opening, the *anus*.

These homologies are, however, associated with a complexity of organization unrepresented in the Cœlenterates. The Platyhelminths all present a typical bilaterality of form, and show furthermore a well-marked antero-posterior as well as, in most cases, a dorso-ventral differentiation. The body is usually flattened and more or less vermiform, whence the name of the group, and is adapted to a creeping habit, certain parasitic forms, and some Nemerteans which live buried in sand, being the only forms not presenting such a mode of life.

The greatest contrast to what occurs in the Cœlenterates however, is presented by the development of compact organs. The nervous system is no longer an altogether diffuse tissue, scattered in a thin layer throughout the body, but a large number of ganglion-cells are aggregated into a compact mass, the brain, embedded in the mesoderm parenchyma near the anterior end of the body, and from this there pass backwards two or more longitudinal cords of nerve-fibres which give off branches extending to all parts of the body and forming a network below the basement-membrane from which the peripheral muscles derive their nerve-supply. In some cases nerves have been observed to pass from this network through the basement-membrane to come into connection apparently with nerve-cells lying between the inner ends of the ectoderm-cells as well as with sensory cells resembling in general form those already described as occurring in the Cnidaria. It must not be understood, however, that the ganglion-cells are limited in their distribution to the lower layer of the ectoderm and the brain; on the other hand, they are scattered along the nerve-cords which arise from the brain, the Platyhelminths presenting in the structure of their nervous system a condition intermediate between the diffuse arrangement of the ganglion-cells seen in the Cnidaria and the more perfect aggregation occurring in higher types.

An excretory system of branching tubes traversing the mesoderm parenchyma and opening to the exterior is also present. It consists usually of two main tubes, nephridia, from which numerous branches arise, terminating in blind funnel-like extremities (Fig. 70, *f*) lying in the meshes of the parenchyma. Each *funnel* (Fig. 78, *B*) is closed by a single cell (*tc*), from which there projects into the tube a bundle of cilia (*fl*), and which, from the resemblance of the motion of these cilia to a flame flickering in the wind, is known as a *flame-cell*. The larger tubes are lined by a layer of cells which seem, in certain cases at least, to be ciliated, but the smaller branches consist of a series of cells succeeding one another in a single row, the canal running through the centres of the cells and being thus intra-cellular. The tubes throughout the entire system contain a fluid in which particles resembling guanin in their behavior to reagents have been seen, and there is little room for doubt but that the tubes have an excretory function.

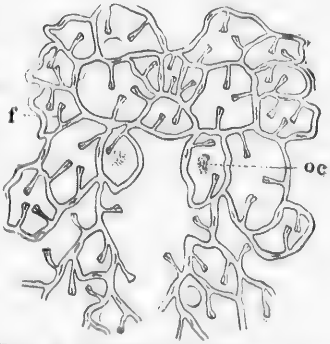

FIG. 70.—EXCRETORY SYSTEM OF THE ANTERIOR PORTION OF THE BODY OF *Planaria montana* (after CHICHKOFF).
f = funnel. *oc* = eye.

Finally, a complicated reproductive apparatus (see Figs. 68-70) is present, the Platyhelminths being for the most part hermaphrodite. The testes consist of from two to many globular bodies whose ducts unite to form two *vasa deferentia* opening to the exterior through a muscular intromittent organ, and sometimes dilating to form reservoirs, the *seminal vesicles*, in which spermatozoa may be stored up until required for fertilization. The female apparatus is somewhat more complicated. The ovaries are usually two in number and their products pass to the exterior through special tubes, the *oviducts*, which may be exceedingly long and with the terminal portion dilated to form a *uterus* in which the ova may pass through certain stages of their development. Connected with the oviducts there is usually a pouch-like structure, the *seminal receptacle*, for the reception of spermatozoa, and furthermore they may receive the products of two other glands which supply the yolk and the shell for the ova. The yolk-glands are in some cases very voluminous, forming what is termed the *vitellarium*, and have been apparently developed by the separation of a portion of the original ovary, their cells, which manufacture the yolk material, being accordingly equivalent to germ-cells. The evidence for this supposition is derived from the arrangement found in some *Turbellaria* and will be pointed out, together with the variations which the complex of organs presents, in the descriptions of the various groups.

I. CLASS **TURBELLARIA.**

The *Turbellaria* derive their name from the fact that the ectoderm is furnished with cilia, which form the locomotor organs of the animals, whose gliding motion over the surface of the objects among which they live is very characteristic. The majority of the members of the class lead a free life, some in fresh and some in salt water, and some even on land, creeping about on the under surfaces of stones or weeds. A few, however, are parasitic either upon the outside of the bodies of their hosts (*Bdellura*) or in a few cases living in the body-cavity or even being imbedded in the tissues.

In addition to the ordinary ciliated cells the ectoderm contains numerous sensory as well as gland cells. Special glands secrete in most of the groups peculiar rod-like bodies which lie scattered about in the ectoderm between its component cells or may project more or less beyond its surface. These *rhabdites*, as they are termed, are produced as a secretion by cells lying usually in the mesoderm and connected with the exterior by a slender neck passing through the basement-membrane, the rhabdites thus making their way to the exterior. The rhabdite-cells are ectodermal, their position in the mesoderm being quite secondary, and in fact in one group they are confined to the ectodermal layer. The function and nature of the rhabdites have been variously interpreted, some authors considering them equivalent to the Cnidarian nematocysts, but it seems more probable that they are the condensed secretion of cells which originally produced a mucous substance and by slowly dissolving in water produce a viscid slime of sufficient tenacity to retain organisms coming in contact with it.

In addition to these structures many forms possess *adhesive cells*, columnar cells which produce a strongly adhesive secretion which is poured out in drops upon the free extremity of the cell, recalling in this respect the adhesive cells of the Ctenophores. These cells seem to be of use mainly in enabling the worms to adhere to the surface on which they are creeping, and are especially developed towards the hinder end of the body. Another organ of adhesion in the form of a muscular sucker, situated usually about the middle of the ventral surface, is present in certain marine Turbellaria, but the majority of the members of the group lack such structures.

The nervous system consists of a brain from which a number of nerve-cords arise, varying somewhat in their arrangement in the different orders. Sense-organs of one kind or another are usually present in addition to the widely-distributed sensory cells of the ectoderm. A large number of forms possess eyes, which in some Polyclads may be exceedingly numerous, and usually consist of a patch of pigment lying in the mesoderm and upon which a refractive lens-like structure lies. In a few cases, as in *Microstoma*, the eye is simply a patch of pigment in the ectoderm near the anterior end of the body. An otocyst, consisting of a spherical vesicle filled with fluid and containing an otolith of carbonate of lime, is present in some of the lower Turbellaria, as *Monotus*, and rests directly upon the surface of the brain; these structures probably, as in the Cnidaria, are sense-organs of equilibrium rather than of audition. In the Polyclads tentacles are frequently present, sometimes capable of being retracted and serving as organs of touch, and in certain Rhabdocœls there is a ciliated depression on each side of the head richly supplied with nerves forming what has been considered an olfactory organ.

1. Order **Acœla**.

The Acœla form a group of lowly-organized Turbellaria exclusively marine in habitat and leading an active and free existence. They all possess a mouth (Fig. 71, *m*) situated on the ventral surface and leading into a short pharynx, though in some forms this may be absent; but beyond this there is no trace of a digestive tract, the food passing from the pharynx into the parenchyma (*p*), where it is digested. Owing to the lack of a digestive tract these forms are strictly two-layered (Fig. 69, *A*), only the ectoderm and mes-endoderm being represented, and consequently are exceedingly interesting as indicating the manner in which the differentiation of the triploblastic condition has been derived from the diploblastic.

The nervous system has been described in *Convoluta* as consisting of a bilobed ganglion surrounding the otocyst, and in front of this and united to it by commissures is a second pair of ganglia. From the anterior ganglia there arise by a common stem two nerves on each side which pass backwards, one along the edge of the body and the other a little internal to it, while the posterior ganglionic mass gives rise to two nerves which pass backwards, one on each side of the median line. All six nerves send off numerous transverse branches which unite to form with the nerve-cords a square-meshed network. In addition to the single otocyst (Fig. 71, *ot*) two pigment-spots lying in the ectoderm and representing light-percipient organs (*e*) are present, as well as a peculiar refractive highly-movable organ, lying in the median line on the anterior margin of the body, which is supposed to be tactile in function.

No excretory apparatus has as yet been described for the Acœla, but a reproductive system with some interesting peculiarities occurs. The male apparatus consists of numerous spherical testes (*t*) whose ducts unite to two vasa deferentia, dilating below to form the seminal vesicles (*vs*) and uniting in the muscular intromittent organ. The female organ is, however, relatively simple, consisting of two club-shaped ovaries (*ov*) whose short oviducts open almost directly to the exterior near the posterior end of the body by a pore (♂♀) common to both male and female apparatus. There is no vitellarium, no shell-gland, no seminal receptacle, and no special uterus, a state of affairs indicating great simplicity of structure compared with what is found in the other orders.

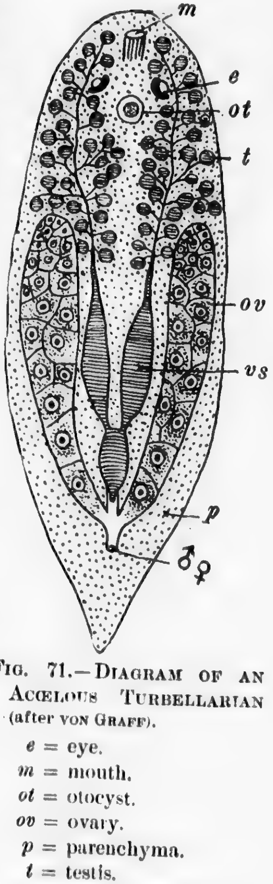

FIG. 71.—DIAGRAM OF AN ACŒLOUS TURBELLARIAN (after VON GRAFF).

e = eye.
m = mouth.
ot = otocyst.
ov = ovary.
p = parenchyma.
t = testis.
vs = vesicula seminalis.
♂♀ = reproductive orifice.

2. Order **Alloiocœla.**

The members of this order are marine with the single exception of *Plagiostoma lemani*, which is found in the deep waters of the Swiss lakes. They present a distinct advance upon the Acœla in that a well-defined digestive tract is present (Fig. 69, *B*), the interval between it and the peripheral musculature being completely filled up by the usual parenchyma and the organs imbedded in it. These forms are then triploblastic, possessing well-defined ectoderm, mesoderm, and endoderm, a condition found in all the higher orders.

The mouth varies somewhat in position, lying either near the anterior or the posterior end of the body, and opens into a *pharyngeal pouch*, whose walls are thickened by muscle-fibres in such a way as to form a somewhat bulbous mass sharply marked off from the parenchyma which surrounds it. In *Monotus*, however, the pharynx is more developed, projecting as a strong circular fold into the pharyngeal pouch and forming what is termed a *plicated pharynx*. This at its inner extremity communicates with the sac-like intestine, usually quite simple but occasionally somewhat pouched, and terminating, as in all the Turbellaria, blindly.

The nervous system consists of a bilobed ganglionic brain-mass from which pass backwards two nerve-cords which may (*Monotus*) or may not present transverse anastomosing branches, and in addition a number of smaller branches pass forward to be distributed to the anterior end of the body. Eyes, consisting of pigment-spots seated upon the brain, are frequently present, and in *Monotus* an otocyst is found, while lateral ciliated depressions on each side of the head occur in *Plagiostoma*.

The excretory system is present, but presents no notable departures from the typical arrangement. As regards the reproductive organs, the testes resemble those of the Acœla, but the ovaries are comparatively small and the separate vitellaria are large and sometimes branched, opening into a cavity, the *genital atrium*, common to them, the oviducts and the intromittent organ, and communicating with the exterior by a single median pore situated near the posterior end of the body. In a few forms the vitellaria are not differentiated from the ovaries, presenting a condition similar to that found in the Acœla.

3. Order **Rhabdocœla.**

The Rhabdocœla are found both in fresh and salt water and are usually small. They possess a distinct tubular digestive tract (Fig. 69, *C*, *d*) without lateral pouches or branches, but the principal characteristic lies in the presence in the parenchyma of large spaces resembling the cœlomic cavities of higher types, a feature not repeated in any other Turbellaria.

The mouth is situated at various regions of the body in different forms, being anterior in *Microstoma*, while in *Mesostoma* (Fig. 72) it is situated at the middle of the ventral surface. The walls of the pharyngeal pouch (*ph*) may be quite simple, as in the Acœla which possess a pharynx, or may present a muscular thickening forming a bulbous pharynx, but no further complexity occurs, although in certain forms, such as *Prorhynchus*, the pharynx is capable of being protruded from the mouth, acting probably as a delicate tactile organ.

The nervous system (*n*) is essentially similar to that of the Alloiocœla; two or four eyes (*oc*) frequently occur, though otocysts are wanting, while the ciliated depressions on the side of the head supposed to be olfactory in function occur in *Microstoma* and *Prorhynchus* and allied forms.

The excretory system consists occasionally of a single nephridium with numerous branches which open near the posterior end of the body, but more usually two main tubes are present opening near the middle of the body either directly to the exterior or into the pharyngeal pouch (*Mesostoma*), though in some cases they unite near the posterior end of the body into a single tube which opens to the exterior by a single median pore (*Vortex*).

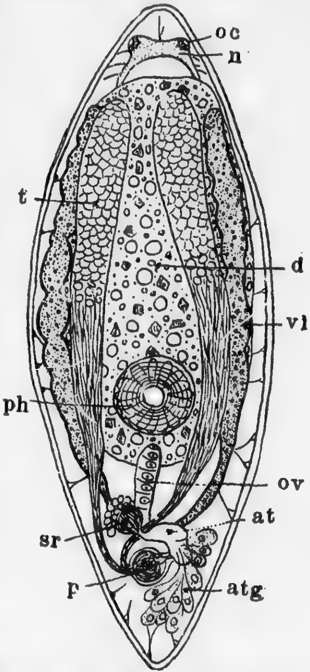

FIG. 72.—A RHABDOCŒLOUS TURBELLARIAN, *Mesostoma splendidum* (after VON GRAFF).

at = atrium.
atg = atrial gland.
d = intestine.
n = brain.
oc = eye.
ov = ovary.
p = penis.
ph = pharynx.
sr = receptaculum seminis.
t = testis.
vi = yolk-gland.

The reproductive system presents considerable variation in the structure of the female apparatus, but the testes (*t*) are uniformly two simple club-shaped bodies uniting below to form a common seminal vesicle. The female apparatus may consist of a single ovary (*ov*) combined with a vitellarium or of two such structures, but usually there is a separation of the vitellarium (*vi*). In the more complicated cases there is but a single small ovary opening almost directly into the genital atrium, which receives also in addition to the intromittent organ the ducts of the two vitellaria. Its walls are furthermore pouched out into a seminal receptacle and a sac-like cavity which serves as a uterus, while a peculiar muscular sac, lined by a strong cuticle, the *bursa copulatrix*, serves for the reception of the intromittent organ during copulation. As stated, however, numerous variations from such a condition occur, and it is not possible to describe any one arrangement characteristic of all the Rhabdocœls.

4. Order **Tricladea.**

The Triclads constitute a group of forms with very definite structural peculiarities, occurring principally in fresh water (*Planaria*, *Dendrocœlum*, *Phagocata*), though a few forms are terrestrial (*Bipalium*), and a still smaller number marine (*Gunda*, *Bdelloura*). As a rule they are elongated in form, one of the terrestrial species reaching a length of 2 cm., and are for the most part free-living, though *Bdelloura* and *Syncœlidium* are ectoparasites of the King-crab (*Limulus*). The mouth is situated in all cases behind the middle of the body and leads into a somewhat capacious pharyngeal pouch (Figs. 69, *D*, and 73, *ph*) in which lies a muscular cylindrical pharynx capable of protrusion from the mouth-opening. The digestive tract at the base of the pharynx divides into three branches, one of which passes forward in the median line, giving off simple or branched diverticula on both sides, while the other two pass backwards on either side of the pharyngeal pouch, giving off diverticula only from the outer side. The intestinal branches, whose number has suggested the name of the order, and their diverticula are imbedded in a compact parenchyma, no well-marked cœlomic spaces being present (Fig. 69, *D*).

The nervous system consists of a bilobed brain lying in the anterior part of the body and from which two nerve-cords pass backwards, united at intervals by cross-commissures and giving off on their outer sides branches which anastomose with one another, forming a network.

In *Gunda segmentata* the transverse commissures agree in number and arrangement with the lateral branches on the one hand and with the diverticula of the intestine on the other, the arrangement of the two systems producing an appearance of metamerization which is most striking, especially as it affects as well the excretory and reproductive systems. In this form an indication is afforded of the manner in which the more pronounced and typical metamerization of the higher types has been produced by the more or less completed multiplication of the organs and the integration of the parts so formed into a metamere (see p. 43).

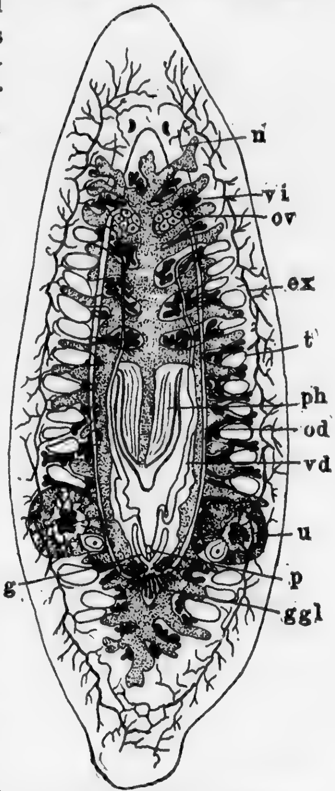

FIG. 73.—A TRICLAD TURBELLARIAN, *Syncœlidium pellucidum* (after WHEELER).

ex = excretory system.
g = accessory gland.
ggl = vaginal glands.
n = nervous system.
od = oviduct.
ov = ovary.
p = reproductive orifice.
ph = pharynx.
t = testis.
u = uterus.
vd = vas deferens.
vi = yolk-gland.

Eyes are usually present, frequently provided with lenses, and, though usually two in number, may be very numerous and situated along the margin of the body. No otocysts occur, and the sides of the anterior end of the body are in some forms produced into more or less elongated processes which may possibly be mainly sensory in function, while behind them are areas of strongly ciliated cells richly supplied with nerves and presumably corresponding with the ciliated depressions occurring in the same region in the Alloiocœla and Rhabdocœla.

The excretory system differs from that of the lower orders in that the two longitudinal nephridia open on the dorsal surface of the body by numerous pores, which in *Gunda* correspond in number with the intestinal diverticula and nerve-commissures. The reproductive apparatus consists of numerous testes (Fig. 73, *t*), as in the Acœla (arranged metamerically in *Gunda*), whose ducts unite to vasa deferentia (*vd*) uniting in the muscular intromittent organ which projects into the genital atrium. Two small ovaries (*ov*) occur in the anterior end of the body, their large oviducts passing backwards to unite in a muscular *bursa copulatrix*, and receiving at intervals the secretion of numerous lateral diverticula which constitute the vitellarium (*vi*). A pouch-like diverticulum of the atrium serves as a uterus, and the single median orifice (*p*) of the atrium lies near the posterior end of the body behind the mouth-opening.

5. Order **Polycladea.**

The Polyclads are exclusively marine and assume various forms, some being quite elongated while others are flat leaf-like expansions. Compared with the members of the other orders they may be said to be as a rule large, though few reach the length which has been mentioned for some land Triclads. The mouth varies greatly in position, as in the Rhabdocœls, and opens into a spacious pharyngeal pouch containing a plicated pharynx (Fig. 73, *ph*). The intestine consists of a central cavity, into which the pharynx opens at its inner end and from which numerous branches (hence the name of the order) pass off into the compact parenchyma, where they branch and may anastomose with one another to form a network. The nervous system presents a somewhat similar condition, the bilobed brain (*ce*), usually situated near the anterior end of the body, giving off a number, usually six, of nerve-cords which become lost in a wide-meshed network ramifying through the body-tissues. Eyes are usually present, frequently in enormous numbers, and furthermore in many forms (*Planocera*) tentacles arise from the dorsal surface or else from the margin near the anterior end of the body. As in the Triclads otocysts are wanting, nor have ciliated lateral depressions been described as occurring in the order.

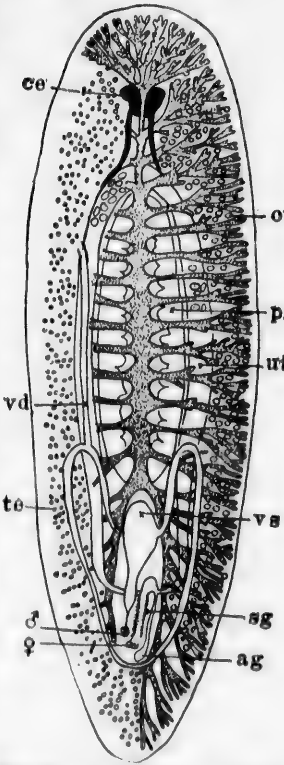

Fig. 74.—A Polyclad Turbellarian, *Leptoplana alcinoi* (after Lang).
ag = accessory gland.
ce = cerebral ganglion.
ov = ovary.
ph = pharynx.
sg = shell-gland.
te = testis.
ut = uterus.
vd = vas deferens.
vs = vesicula seminalis.
♂, ♀ = male and female orifices.

Little is known concerning the excretory system. The reproductive system differs from that of the other orders in that the male and the female apparatus each possess a separate opening (♂ and ♀), there being no genital atrium common to both. Both apertures lie behind the mouth-opening, near the posterior end of the body, the male apparatus opening anteriorly to the female. The former is similar in structure to what has been described for the Triclads. The female apparatus possesses no vitellarium, and the ovaries (*ov*) are very numerous, lying in the lateral parts of the body, their various ducts uniting to form wide canals which serve as uteri (*ut*). These open into a single tube, the *vagina*, which receives the secretion of the numerous glands (*sg*) which form the shell-gland.

In some forms there is situated about the middle of the ventral surface of the body a muscular sucker which serves as an organ of adhesion. Since the presence or absence of this organ is in either case associated with the occurrence of other important structural peculiarities, the order has been divided into two suborders—the *Cotylea*, provided with a sucker (*Thysanozoon*, *Eurylepta*), and the *Acotylea*, in which it is absent (*Planocera*, *Leptoplana*).

Reproduction of the Turbellaria.—Non-sexual reproduction is not characteristic of the Turbellaria, though it occurs in certain Rhabdocœls. In *Microstoma* a transverse partition, consisting of two closely-applied lamellæ, forms, extending from the outer wall of the body to the wall of the digestive tract, which it constricts slightly without dividing. Later a constriction of the outer surface of the body appears, the two lamellæ of the partition separate slightly, and the individual lying behind the partition develops a new mouth and pharynx and a new brain, so that it resembles exactly the anterior individual with which it is directly connected by the uninterrupted digestive tract. Before these processes are complete, however, they are repeated in each of the two individuals, so that a chain of four imperfectly separated individuals results, and by further repetitions of the process chains of 8, 16, or 32 individuals may arise, each provided with mouth, pharynx, and brain, the anterior individual possessing the original structures, and all connected by the digestive canal which runs uninterruptedly through the entire chain (see Fig. 28). Eventually the various individuals separate from one another and become sexually mature.

The sexual method, however, plays a much more important part in the life-histories of the Turbellaria. The development of the three lower groups has not as yet been as thoroughly investigated as is desirable, but the phenomena which occur in the Triclads, and especially in the Polyclads, have been followed. The Triclads deposit their ova in chitinous cocoons, which contain, besides the ova proper, large numbers of amœboid cells, originating in the vitellarium-pouches of the parent, and serving as food for the young embryo. In association with this condition of affairs many peculiarities of segmentation and growth occur in the Triclad embryos, all of which must be considered as secondary adaptations.

In the Polyclads, however, a more primitive state of affairs occurs, the food-yolk being incorporated with the protoplasm of the ovum, a more or less distinct irregular segmentation resulting from its telolecithal arrangement (p. 53). The diploblastic condition arises by an invagination either of the embolic or epibolic type, but at an early period of the segmen tation the cells which are to form the mesoderm are separated off from those from which the ectoderm and endoderm are to be derived, so that even before the invagination all the three layers are represented. This, however, is to be regarded as a precocious segregation of the germ-layers, and even within the limits of the few forms whose embryology is known considerable variations in the time and manner of the differentiation of the mesoderm occur. The result of the invagination is in some cases a solid, bilaterally symmetrical, ciliated embryo consisting of a layer of ectoderm enclosing a central mass of endoderm and mesoderm, in the interior of which a cavity appears surrounded by the endoderm. A depression appears on the ventral surface, which, deepening, finally unites with the enteron and forms the pharyngeal pouch, and gradually the characters of the adult are assumed.

In some forms whose ova are provided with comparatively little yolk the embryo leads from an early period a free-swimming existence, and in accordance with this a specialized form has been acquired and a slight metamorphosis is necessary for the conversion of this *larva* into the adult condition. In *Stylochus* the embryo develops into what is known as *Goette's larva*, a bilateral ciliated structure with an anterior and posterior tuft of strong sensory hairs, while from the ventral surface on either side of the mouth there hang down two ciliated ear-like lobes or lappets. In another form (*Thysanozoon*) these lappets are much more developed, passing round to the dorsal surface of the body, and their edges are drawn out into four or eight lobes, one of which lies in front of the mouth and another on the dorsal surface, the other two or six lying at the sides of the body and being arranged symmetrically on either side. It seems probable that this larva, known as *Müller's larva* (Fig. 75), may be traced back to a condition such as that described in Goette's larva, the two lappets of that form having united in front of the mouth, while their lines of attachment have become more

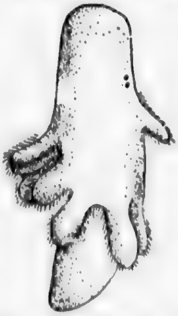

FIG. 75.—LARVA OF *Thysanozoon*, Müller's Larva (after LANG).

and more oblique until what were originally the posterior edges of the lappets meet on the dorsal surface. The edges of the lobes of the lappets are fringed with long cilia, and consequently a lobed præoral band of cilia is produced. These larvæ pass into the adult form by gradually becoming more and more flattened dorsoventrally, the ciliated lappets or lobes at the same time growing smaller and smaller until they finally disappear.

Relationships of the Turbellaria.—A relationship of the Turbellaria, especially of the Polyclads, with the Ctenophores has been advocated within recent years, and through this relationship genetic affinities with the Cnidaria have been sought. The question of the affinities of the Ctenophores has already been discussed, and it has been pointed out that it is probable that, instead of being a connecting link between the Cnidaria and the Turbellaria, they are rather highly modified Turbellaria adapted to a pelagic life. In this sense the idea of a genetic affinity between the Turbellaria and Ctenophores may be correct, though it seems probable that the Polyclad affinity should be given up and the relationship sought for among Alloiocœlan forms.

The Ctenophore-Polyclad theory necessarily viewed the Polyclads as the most primitive Turbellaria, and came into contact in this way with the more simple organization of the *Acœla*, *Alloiocœla*, and *Rhabdocœla*, a difficulty which was avoided by assuming that these were degenerate groups derived from Polycladan ancestors. No good grounds for such an assumption exist however, nothing in the mode of life suggesting a cause for degeneration; and until embryological evidence of degeneration is obtained, it is preferable to consider their simplicity primitive.

This latter view is strengthened if it harmonizes with a probable phylogeny. It has already been pointed out that the solid embryo or *sterrula* is to be recognized as an ancestral form of the Cnidaria. With such an ancestral form the Acœla show affinities in the absence of a differentiation of the central mass into well-defined endoderm and mesoderm. The localization of a definite region for the ingestion of nutrition would lead to the formation of a mouth in the Sterrula, just as it has done in the *Flagellata*. The differentiation of muscle-fibres from the mesendodermal cells would naturally follow the assumption of a creeping habit, so that it is only the possession of a definite nervous system imbedded in the mesoglœa (in which tissue, however, Cnidarian characteristics are yet discernible, as already pointed out) and the occurrence of a complicated reproductive apparatus that render a close comparison with the Sterrula difficult; but even the explanation of the presence of these structures makes fewer demands upon our ideas of developmental possibilities than does the assumption that the *Acœla* owe their peculiarities to degeneration.

Upon this view of the phylogeny the *Acœla* are united with the Cœlentera only through the Sterrula ancestor common to both, or more probably through an ancestor in which the mouth had developed, as well as a slight differentiation of muscle-fibres, but in which no hollowing out of an enteron had yet occurred. This appearing in a primitive acœlan form gave rise to the *Alloiocœla* from which two divergent lines of descent arose, one leading to the Rhabdocœls and the other to the Triclads and Polyclads.

If this be the true phylogeny of the class, some evidence of it ought to be found in the embryological history of some of the higher members of the group in accordance with what is termed the *Biogenetic law*, which is to the effect that an individual in its development recapitulates more or less accurately its phylogenetic development, or, to put it more briefly, *the ontogeny is a recapitulation of the phylogeny.* Secondary modifications, especially in the form of the abbreviation or omission of certain stages, may intervene in the individual development, forming what are termed *cenogenetic modifications*, but notwithstanding exceptions produced in this way the law is of general application.

In *Stylochus* the young larva is a solid body without any enteron and represents, therefore, an Acœlan stage of development; later the central mass becomes hollowed out to form an enteron whose walls are not at first clearly marked off from the surrounding parenchyma, and a representation of the Alloiocœlan condition results, from which the Polyclad condition gradually develops. Consequently in *Stylochus* the ontogeny indicates a primitive nature for the *Acœla*, and agrees with the phylogeny which has been outlined above. It must be recognized, however, that all reconstructions of the phylogeny of the Turbellaria and all views as to their affinities to the Cnidaria must be accepted with much reservation, until the much-needed facts as to the developmental history of the *Acœla* and *Alloiocœla* are available.

II. Class **Trematoda.**

The Trematodes or Fluke-worms are throughout parasitic. *Suckers* are present in all, consisting of cup-like depressions whose walls are richly supplied with muscle-cells, by the contraction of which a vacuum is formed, and in many forms, in addition to these, chitinous hooks occur. The suckers vary in number from one (*Monostomum*) or two (*Distomum*, Fig. 76) to several (*Polystomum*), and at the bottom of one situated at the anterior extremity of the body is the mouth-opening. This leads into a tubular œsophagus whose walls are thickened near its anterior end to form a muscular *pharyngeal bulb* which functions as a pump for the ingestion of the nutritive fluids of the host. At its posterior extremity the œsophagus branches into two limbs which are continued backwards, in some cases giving off secondary branches, to near the posterior end of the body, where they either end blindly or unite together in the middle line (*Polystomum*) to form a loop.

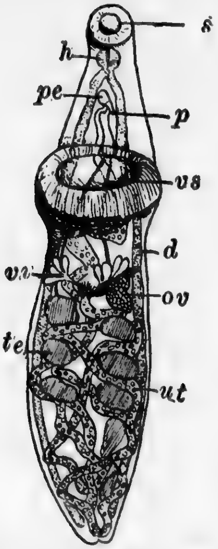

FIG. 76.—*Distomum cygnoides* (from a drawing by C. LANGENBECK).
as = anterior sucker
d = intestine.
ov = ovary.
p = reproductive orifice.
ph = pharyngeal bulb.
pe = cirrus.
te = testis.
ut = uterus.
vi = yolk-gland.
vs = ventral sucker

The body is covered by a distinct cuticle secreted by the ectodermal cells, which in the adult may undergo a considerable amount of degeneration, or probably in some cases the cuticle is formed in part by the transformation into chitin of the ectoderm. Spiny elevations of the cuticle are present in many forms, and the large chitinous hooks which occur in many ectoparasitic forms are but further developments of these structures. Below the ectoderm lies the usually thin basement-membrane, below which again lie the circular and longitudinal peripheral muscle-sheets, and between the intestine and these muscles is the parenchyma traversed by dorsoventral muscle-bundles and having imbedded in it the reproductive and other organs of the body.

The nervous system (Fig. 77) consists of a transversely elongated ganglion lying dorsal to the œsophagus—usually between the bottom of the anterior sucker and the pharyngeal bulb. The ganglion is somewhat swollen at each extremity, indicating its origin by the approximation of two ganglionic masses, and from these thickenings nerves arise which pass both forward and backward. The anterior nerves are short and slender, and supply the musculature of the anterior sucker and the sides of the anterior end of the body, while the posterior nerves are much stronger and longer and vary from two to six in number; in the latter case four run along the ventral surface of the body, two on each side of the middle line, the other two having a more dorsal position, while when only two are present they correspond to the two more median ventral nerves of this arrangement. Sense-organs are but feebly developed as a rule, especially among the endoparasitic forms, but in some ectoparasites eyes are present consisting usually of four spots of pigment seated upon the brain-ganglion and sometimes provided with a lens-like structure.

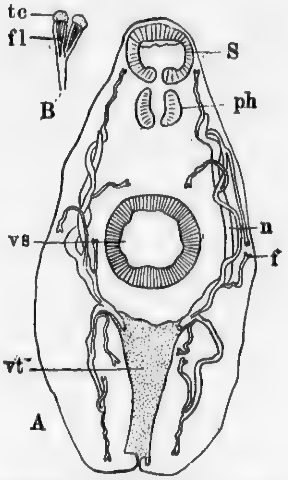

FIG. 78.—EXCRETORY SYSTEM OF TREMATODE, *Distomum divergens* (after FRAIPONT).

A, entire system; *B*, terminal funnels.

f = funnel.
fl = flame of cilia.
n = main trunk.
ph = pharyngeal bulb.
s = anterior sucker.
tc = terminal cell.
vs = ventral sucker.
vt = contractile vesicle.

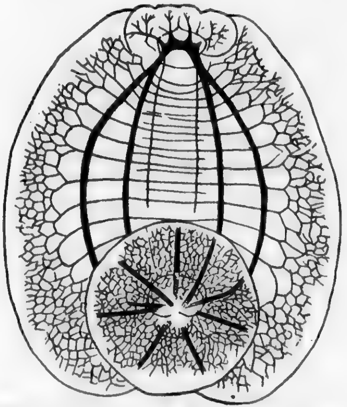

FIG. 77.—NERVOUS SYSTEM OF TREMATODE, *Tristomum molæ* (after LANG).

The excretory apparatus (Fig. 78) consists, as is usual in the Platyhelminths, of two longitudinal, more or less irregularly twisted tubes (*n*) from which arise the funnel-bearing branches (*f*). A peculiarity of the Trematodes is, however, the union of the two longitudinal tubes in a terminal vesicle (*vt*) which opens to the exterior at the hinder end of the body by a single pore.

The reproductive system is exceedingly complicated, though essentially similar to that of the higher Turbellaria. It opens to the exterior by two pores lying close together on the ventral surface rather nearer the anterior than the posterior end. The male apparatus consists in the *Polystomeæ* of numerous closely-aggregated testes, or else, as in the *Distomeæ* (Fig. 76), of only two situated in the posterior half of the body; the ducts from the testes pass forwards towards the genital pore, near which they unite to form a sac-like seminal vesicle, from whose anterior end the single vas deferens is continued on towards the pore, passing in the latter part of its course through a muscular protrusible intromittent organ, the *cirrus*. The ovary is single, and its duct shortly after leaving it receives the ducts coming from two yolk-glands situated one on either side of the body, and is surrounded at about the same region by a shell-gland, consisting of a number of unicellular glands arranged in a radiating manner around the oviduct. Beyond its union with these ducts the oviduct either runs almost directly to the genital atrium, opening into it in close proximity to the cirrus, or else pursues a winding contorted course through the parenchyma and serves as a uterus or *ootyp*, within which the ova undergo a portion of their development.

From the oviduct in the region where the ducts from the vitellaria and shell-gland open into it one or more canals may arise whose significance is to a certain extent problematical. In the Distomeæ one such canal occurs, and when a seminal receptacle is present it stands in more or less close relations to this canal, known as *Laurer's canal*, which, after a short course, opens to the exterior on the dorsal surface of the body. In some *Polystomeæ* two canals arise from the yolk-ducts and pass forwards parallel to the uterus to open by a number of pores situated on the margin of the body. These canals have been termed the *vagina*, and in some forms are represented by a single canal. In addition to the vagina, however, another canal is present which has been shown in *Polystomum* and *Sphyranura* to open into the digestive tract, and has been homologized with Laurer's canal of the Distomeæ.

It seems pretty certain that the vagina of the Polystomeæ functions in copulation, the genital orifice of one *Polystomum* having been observed to come into contact with the vaginal openings of the other during that act. But the Laurer canals do not seem to have any such function, and it has been suggested that they may serve for the removal of surplus yolk-material produced in accordance with the favorable conditions for nutrition offered by the parasitic mode of existence of the Trematodes.

Two orders may be recognized as occurring in the Trematoda.

1. Order **Polystomeæ.**

The Polystomeæ are for the most part ectoparasites and present fewer signs of degeneration than do the endoparasitic members of the class. The apparatus for adhering to their hosts is usually strongly developed, several suckers usually being present, as, for instance, three in *Tristomum* and seven in *Polystomum integerrimum* (the latter parasitic in the urinary bladder of the Frog), and in addition a number of chitinous hooks may occur, as in *Gyrodactylus* and *Sphyranura* (the latter parasitic on the skin of *Menobranchus*). In accordance, too, with their mode of life, sense-organs in the form of eyes and probably of tactile papillæ on the skin occur, and furthermore the processes of development are much simpler than in the endoparasites, as will be seen later.

Some peculiar anomalies occur in the life-histories of some of the Polystomeæ, as, for instance, in the *Gyrodactylus*, which lives upon the gills of the Carp. It is a viviparous form, and the young while still within the body of the parent may already have become mature and contain young likewise, which again may contain ova in course of development, four generations being thus enclosed one within the other. *Diplozoon*, which lives likewise on the gills of Cyprinoid fishes, is peculiar in that at the time of sexual maturity two individuals become fused with one another in the form of an X, the fertilized ova giving rise to a single form formerly known as *Diporpa*.

2. Order **Distomeæ.**

This order includes endoparasites which show a more marked degeneration than do the members of the preceding order. Eyes may be present in the young but are absent in the adult, and furthermore a very complicated metamorphosis is passed through in the development. The suckers for adhesion to the host are either one (*Monostomum*) or two (*Distomum*), and as a rule no chitinous hooks are present.

Among the more interesting members of this order are *Distomum hepaticum*, a large form measuring 2–3 cm. in length and inhabiting the bile-ducts of Sheep, in which it produces what is termed the "Rot," which, in the low-lying pastures of England and the Continent, is frequently the cause of the destruction of large numbers of sheep. In exceptional cases it has been known to occur in man. In Egypt, however, the Fellaheen are not unfrequently attacked by another form, *Distomum hæmatobium*, which is peculiar in that, contrary to the rule, the sexes are separated in different individuals. The margins of the body of the male are rolled inwards on the ventral surface, forming a tube within which the more slender female lives. Associated in pairs in this way, they are found in the blood of the portal vein and its connections and pass to the ureters and bladder, in whose mucous membrane they deposit their ova, thus producing an inflammation, accompanied by suppuration, of these organs.

Development of the Trematodes.—The ova of Trematoda consist of two distinct parts, a germ-cell, the product of the ovary, surrounded by a mass of food-material, the secretion of the vitellaria, the whole being enclosed in a shell formed by the shell-gland. In the Polystomeæ the development, as a rule, is entirely carried on outside the body of the parent, the stalked ova being attached to the body of the host, though *Gyrodactylus* is viviparous. In the Distomeæ, however, the reverse is the rule, the ova undergoing a certain part of their development in the uterus of the parent, and leaving the egg shortly after its extrusion as a larva, sometimes ciliated, sometimes provided in the place of the cilia with a structureless cuticle, and furthermore in these endoparasites there occurs a remarkable alternation of generations of the kind already referred to as heterogony (see p. 61).

The heterogony may be of various degrees of complexity. It begins, however, in all cases with the embryo (Fig. 79, *A*), which may be a free-swimming ciliated organism provided with a short pouch-shaped intestine and with a mouth, and frequently possessing also a nervous system and pigment eye-spot as well as excretory tubes; in other cases, however, as stated, the embryo is destitute of cilia, usually in this case being provided with one or more spines at the mouth-end of the body, and all gradations of degeneration of the eye-spot and nervous system, as well as of the excretory tubes and digestive system, may be observed. In all, however, the space between the more or less developed digestive tract and the body-wall is occupied by numerous unspecialized cells (*gc*), which are in reality germ-cells or ova capable of undergoing a parthenogenetic development. Eventually this larva makes its way into the interior of an animal of some kind, usually a Mollusk, and there undergoes a further development, either retaining its digestive apparatus and elongating somewhat to form a *Redia* (Fig. 79, *B*), or becoming an oval sac without mouth or digestive tract, the *Sporocyst.* The Redia is a much more highly organized form than the Sporocyst and is frequently capable of motion, two blunt projections near the hinder end of the body serving as supports in a somewhat similar manner to the sucker-like feet of caterpillars. It adheres to the wall of a cavity of its host, from which by energetic action of its muscular pharynx it is able to absorb nutrition.

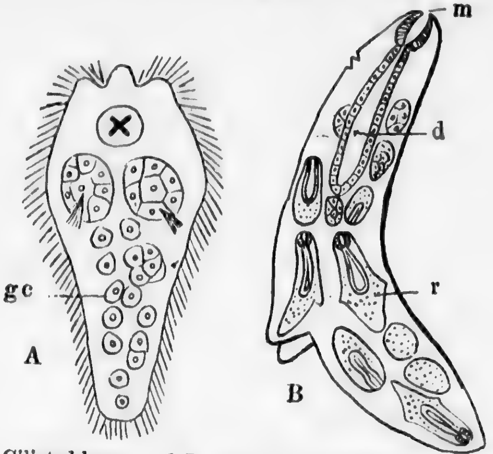

FIG. 79.—*A*, Ciliated larva, and *B*, Redia of *Distomum hepaticum* (after LEUCKART).

d = intestine.
m = mouth.
gc = germ-cells.
r' = second generation of Rediæ.

From this stage onwards the development varies in complexity in various forms. It is simplest in *Monostomum mutabile,* whose ciliated embryo, while still free-swimming, contains within it a small sexually immature *Monostomum,* and after it has made its way into the interior of its Molluscan host the young *Monostomum* becomes encapsuled in the tissues of its host. The mode of origin of this immature form has not as yet been observed, but there is no reason for doubting that it is the result of the parthenogenetic development of one of the germ-cells which occur in the body-cavity of the embryo. So long, however, as it remains in the tissues of the Mollusk it undergoes no further development; it can only reach maturity in a second host, in this case some water-bird which swallows the Mollusk and its encapsuled parasite, when the latter, its capsule being dissolved by the digestive juices of the bird, is set free, fastens itself to the wall of some of the cavities of its host and becomes sexually mature.

In this species of Trematode but two hosts are required in the life-history; in the majority of the Distomeæ a third occurs, an additional stage of development intervening between the Redia or Sporocyst and the encapsuled immature worm. The germ-cells of the Redia or Sporocyst while in the interior of the Mollusk develop into a form resembling an immature Distome, but provided with a mobile muscular tail whose axis is formed by a fibrous rod resembling somewhat in appearance the Vertebrate notochord. Such an organism is known as a *Cercaria* (Fig. 80), and when fully developed the Cercaria brood leaves the body of the parent Redia or Sporocyst, makes its exit from the tissues of the Mollusk and leads for a time a free-swimming existence. Eventually the Cercaria makes its way into the body of a second host, usually like the first a Mollusk, and there becomes encapsuled in the tissues, losing at the same time its tail, and it reaches its maturity only after the Mollusk has been swallowed by the definitive host, as was the case in *Monostomum*.

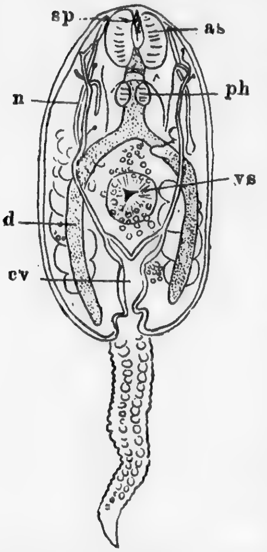

FIG. 80.—*Cercaria armata* (after SCHWARZE).

as = anterior sucker.
cv = contractile vesicle.
d = intestine.
n = nephridial tube.
ph = pharynx.
sp = spine.
vs = ventral sucker.

A still further complexity is found in the Liver Fluke, *Distomum hepaticum.* In this form the free-swimming embryo makes its way into the tissues of a small snail and there becomes converted into a Sporocyst. The germ-cells of the Sporocyst give rise by their development, not to Cercariæ, as in the usual cases, but to Rediæ, and these may give rise under certain conditions to a second brood of Rediæ (Fig. 79, *B, r*). During the summer, however, the Rediæ produce Cercariæ, which, leaving their host, swim about for a short time, and finally encyst themselves, not necessarily in a second Mollusk, but on grass or any other object with which they may come in contact, the tail at the same time being lost. If, now, these encysted forms are swallowed by a sheep, the young Distome makes its way to the bile-ducts of the host, where it becomes mature.

The following schema by R. Hertwig will show the relationships of these different methods of development:

Simple Mode.			Usual Mode.			Complicated Mode.		
I. Generation	Embryo.	Water.	I. Generation	Embryo.	Water.	I. Generation	Embryo.	Water.
	Sporocyst or Redia	I. Host (Mollusk)		Sporocyst or Redia	I. Host (Mollusk)		Sporocyst	I. Host (Mollusk)
						II. Generation.	Rediæ	"
II. Generation			II. Generation	Cercariæ.	Water.	III. Generation	Cercariæ.	Water.
	Encapsuled Distome	I. Host		Encapsuled Distome	II. Host.		Encapsuled Distome	II. Host or on grass, etc.
	Mature Distome	II. Host		Mature Distome	III. Host		Mature Distome	III. Host

In a few Distomeæ a simplification more extensive than that represented in the first columns of the schema occurs, as for instance in the genus *Holostomum*, whose embryo, after making its way into the body of the first host, seems to be gradually metamorphosed into the immature Distome, without any alternation of generations.

A very peculiar life-history is found in *Distomum macrostomum*, which is parasitic in insect-eating birds. The Sporocyst is found in a snail, and is peculiar in that it assumes a branching form, the branches forming a network among the tissues of the host. In the ends of filaments of the network young Distomes develop without the intervention of a Cercaria stage, and by their development and its own growth the terminal branches become of a considerable size, two of them extending into the tentacles of the snail, which thus become enormously distended. The club-shaped structures so formed are abundantly supplied with muscle-fibres, and by vigorous movements finally burst the distended wall of the tentacle, and separating from the Sporocyst fall to the ground. There they move about, resembling an insect larva in general appearance, a resemblance increased by banded markings of green and white, which render them very conspicuous, and they are apt finally to be snapped up by some bird, in whose digestive tract the young Distomes are set free and become mature.

There can be little question but that the simple metamorphosis of the *Polystomeæ* represents the original method of development of the Trematoda, the heterogony characteristic of most *Distomeæ* being a secondary acquisition developed in accordance with their endoparasitism. An idea of the mode in which this alternation of generations has been brought about is furnished by such forms as *Gyrodactylus*, in which the development of the ovum takes place within the body of the parent, the young in their turn developing embryos before being born (see p. 147). This acceleration of sexual maturity, accompanied by parthenogenesis, has brought about the condition seen in the Sporocyst or Redia, which are embryos provided with ova capable of parthenogenetic development. Thus fundamentally the heterogony is a pædogenesis (see p. 60), and may be compared, in a general way, with the formation of a hydroid colony by the budding of a medusa larva.

III. CLASS **CESTODA.**

Like the Trematoda the members of this class are parasites, but are throughout endoparasites, and present a much greater degeneration of structure than is found in the Distomeæ, accompanied by peculiarities of development differing somewhat from what occurs in these forms. The Cestodes or Tapeworms lack all trace of a digestive tract and of a mouth, living in their mature state attached to the wall of the digestive tract of their host, and immersed in the nutritive fluids contained in the intestine.

In some forms, such as *Caryophyllæus* (Fig. 81, *A*), parasitic in the intestine of Cyprinoid fishes, the similarity to a Trematode is very striking, except in the absence of suckers for adhesion and of a digestive tract. The worm consists of a somewhat dilated head, succeeded by a narrower portion which may be termed a neck and gradually enlarges to the rather cylindrical body, which contains a single set of reproductive organs. In *Ligula*, which is found in the intestine of aquatic birds, there is likewise an absence of suckers, but the reproductive organs are present in several sets succeeding one another, without any external indications of a reduplication of parts. In *Triænophorus* the multiplication of the sets of reproductive organs is indicated, however, externally by indistinct constrictions of the body, an indication of a tendency for the individual to separate into a number of parts, each possessing a certain amount of individuality. This tendency reaches its highest development in such forms as *Bothriocephalus* and *Tænia* (Fig. 81, *B*), which consist of an anterior portion, the *Scolex* (Fig. 81, *C*), provided with organs of adhesion in the form of suckers, accompanied or not by chitinous

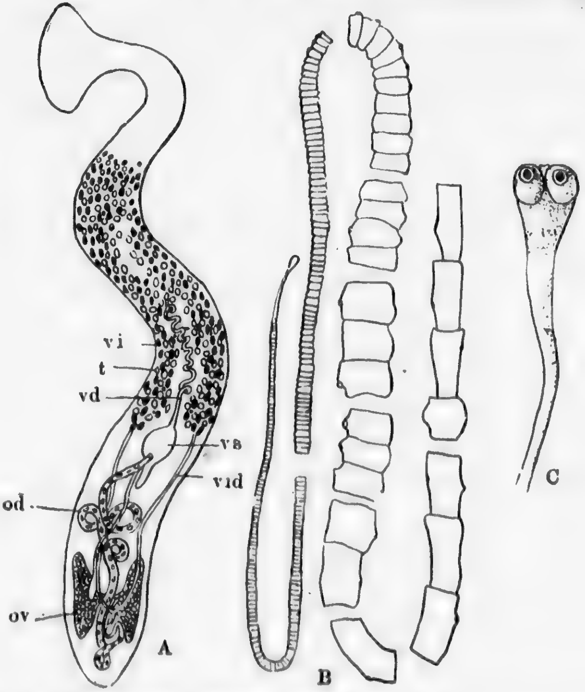

FIG. 81.—*A*, *Caryophyllæus mutabilis* (after STEIN); *B*, *Tænia saginata* (after LEUCKART); *C*, anterior end of *T. saginata* (after LEUCKART).

od = oviduct.
ov = ovary.
t = testis.
vd = vas deferens.
vi = yolk-glands.
vid = yolk-duct.
vs = vesicula seminalis.

hooks and followed by a varying number of segments or *proglottides*, each possessing a set of reproductive organs and capable of separating from its fellows, maintaining for a time an independent life. The proglottides towards the hinder end of the chain or *strobila* are the most advanced in development, and one after another drop off and pass to the exterior of the host's body with the fæces; more anteriorly the proglottides are sexually immature, and still nearer the scolex they are to be found in various stages of formation. In fact the hinder end of the scolex may be regarded as a zone of growth, new proglottides being successively formed at this region. The process of proglottid formation resembles not a little what has been described as the non-sexual reproduction of the Discomedusæ, the scolex corresponding to the parent Scyphostoma and the proglottides to the Ephyræ, the entire aggregation in both cases being termed the Strobila.

The exterior of the body of a Cestode is formed by a cuticle without any trace of cellular structure, and is perhaps to be regarded as a basement-membrane, the ectoderm, originally present, having disappeared. The cuticle varies much in thickness, and is throughout traversed by fine pores which allow of the absorption into the body substance of the nutritive fluids in which the Tapeworm lives, either directly or by permitting the passage to the exterior of fine protoplasmic processes from the subjacent tissue. Special developments of the cuticle in the form of chitinous hooks are frequently present, arranged in some Tænias, for example, in a double circle upon a prominence, the *rostellum*, at the apex of the scolex, and forming a very efficient means of attaching the worm to the wall of the intestine of its host. Beneath the cuticula there is to be found a very thin muscular layer, the peripheral musculature, but the main bulk of the musculature consists of those fibres which traverse the parenchyma. These, especially the longitudinal and transverse ones, are massed into strong bands, the former lying usually exterior to the latter, and both enclosing a central mass which is traversed by weaker bundles of dorso-ventral muscles, and contains the reproductive apparatus.

In connection with the muscular system may be mentioned the suckers which frequently occur upon the scolex, and serve with the hooks, when these are present, to attach the parasite to its host. In *Tænia* these suckers are four in number, and have the form of circular depressions whose walls are richly supplied with muscle-fibres, while in *Bothriocephalus* they have the form of elongated grooves, situated on the edges of the somewhat flattened scolex.

As might be expected from the great development of the muscles, a well-defined nervous system is present. It consists of a brain lying imbedded in the tissues of the anterior portion of the scolex, evidently composed by the union of two ganglionic masses and giving rise to two main nerve-cords, which pass backwards through the entire length of the strobila without interruption (Fig. 82, *n*). So, too, the excretory system (Fig. 82, *ne*) extends through the entire strobila uninterruptedly. It consists of two nephridial tubes, which in the anterior part of the scolex may be united by a cross branch, as they are at the posterior edge of each proglottid, and open to the exterior by a pore situated at the centre of the posterior edge of the last proglottid. After the loss of the original terminal proglottid two pores, corresponding to the extremities of the longitudinal tubes, place the system in communication with the exterior.

The reproductive system (Fig. 82) possesses a complexity similar to what has been described for the Trematoda, and hermaphroditism prevails throughout the class. In the strobilar Cestodes each proglottid contains a complete set of organs, both male and female; the testes (Fig. 82, *te*) are usually very numerous, consisting of small spherical masses scattered through the parenchyma, each being provided with a small duct, which after a short course unites with similar ducts coming from other testes, all finally uniting to a single vas deferens (*vd*), which opens to the exterior after passing through a muscular organ, the cirrus-sac, by the contraction of which its terminal portion, often provided on its inner surface with barbed hooks, is protruded to the exterior as an intromittent organ or cirrus (*c*). The female apparatus varies somewhat in its arrangement. In the majority of forms the ovary is a bilobed organ (*ov*), lying near the posterior end of the proglottid. The oviduct soon after leaving the ovary unites with the yolk-duct (*vid*) coming from the albuminous vitellarium (*vi*), which consists of a number of glands scattered through the parenchyma similarly to the testes. At the point of union with the yolk-duct the oviduct enlarges, receiving at the enlargement the secretion of a number of unicellular glands composing the shell-gland (*sg*). From this enlargement two tubes arise: one, the *vagina* (*va*), runs almost directly forward to open into a chamber, the genital atrium, which contains also the cirrus-sac and communicates directly with the exterior; while the other, the uterus (*ut*), after a somewhat convoluted course opens inde-

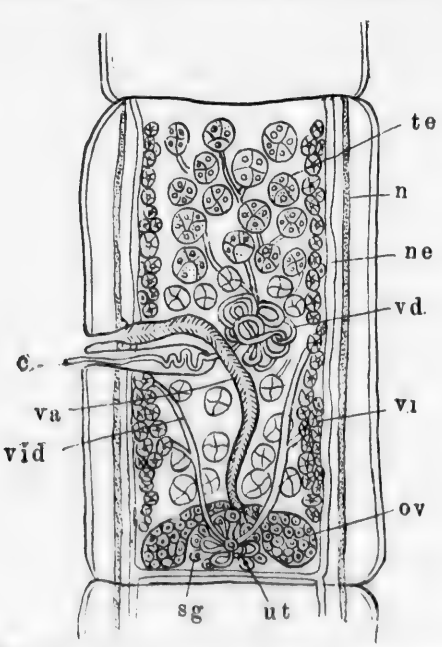

FIG. 82.—PROGLOTTID OF *Tænia filicollis* (after KRAEMER).

c = cirrus.
n = nerve.
ne = excretory canal.
ov = ovary.
sg = shell-gland.
te = testis.
ut = uterus.
va = vagina.
vd = vas deferens.
vi = yolk-gland.
vid = yolk-duct.

pendently to the exterior a little behind the genital pore. The vagina serves as a duct for the spermatozoa during copulation, and corresponds with the canals opening at the sides of the anterior end of the body in the Polystomeæ (see p. 146), while the uterus serves for the retention of fertilized and mature ova. In *Bothriocephalus* the opening of the genital pore is in the middle line of one of the surfaces of the proglottid; in *Tænia*, however, it occurs on the lateral margin of the proglottid, and in some cases each proglottid may have an opening in each of the lateral margins, there being a duplication in such cases of the genital ducts. Furthermore, in the Tænias the vitellarium is much less voluminous than in *Bothriocephalus*, and produces an albumen-like secretion instead of yolk-cells, and in addition the uterus has no special opening to the exterior and is relatively small, though it may become fairly voluminous by its walls being pushed out into pouch-like sacculations by the contained ova.

Development of the Cestoda.—Accompanying the differences in the arrangement of the reproductive apparatus differences in the development are found in the two groups. In *Bothriocephalus* (taking this form again as the example of the one group) the egg is richly provided with yolk-cells, among which the germ-cell lies imbedded. The embryo leaves the egg in the form of a spherical ciliated body, provided with six chitinous hooks, arranged more or less distinctly in pairs. After swimming about for a time the cilia and their cells are thrown off, and the six-hooked embryo makes its way into the body of the first host, where it becomes enclosed in a thin cyst, within which it develops directly to a scolex. If this be swallowed by the second host, the worm fastens itself to the walls of the digestive tract, and soon develops to the sexually mature strobila.

In the Tænias, however, the ova are much smaller, the yolk-cells being replaced by an albumen-like substance, relatively small in amount, and the embryos when they hatch out are destitute of cilia, resembling the six-hooked embryo of *Bothriocephalus* after it has lost its ciliated covering (Fig. 83, *A*). In this condition it makes its way into the primary host, in whose tissues it becomes encysted, and develops in some forms, such as the *Tænia cucumerina* of the dog, whose primary host is the Dog-louse, into a *Cysticercoid*. This resembles a scolex, whose head has been withdrawn into and enclosed by the body, and when it is swallowed by the secondary host, the dog in the instance cited, the head is pushed out, fastens itself to the wall of the digestive tract, and begins to grow and form proglottides. In other cases, however, the posterior part of the scolex into which the head is retracted becomes enormously swollen by the accumulation of fluid within it, forming a large vesicle, into the interior of which the head projects, having become completely invaginated. Such a form as this is termed a *Cysticercus* (Fig. 83, *B*); when it is swallowed by the secondary host the head evaginates, and the cyst remains for some time attached to the hinder end of the scolex, but later disappears, and the formation of the proglottides occurs. Further modifications arise by the formation in the wall of the cyst of not only one but several invaginated heads, forming the *Cœnurus* (Fig. 83, *C*); or even secondary cysts may arise from the inner wall of the original vesicle, and each of them may develop several heads, forming what is known as the *Echinococcus* (Fig. 83, *D*).

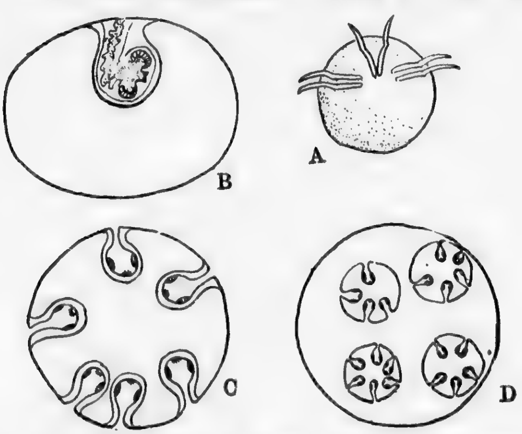

FIG. 83.—*A*, six-hooked embryo of *Tænia*; *B*, diagram of *Cysticercus*; *C*, diagram of *Cœnurus*; *D*, diagram of *Echinococcus*.

Several of the Cestoda are especially interesting from a medical standpoint, inasmuch as they are parasitic in man either during the adult or the larval stage. Among these may be mentioned *Bothriocephalus latus*, which occurs in the human intestine, where it may reach a length of as much as 12 metres, in such cases consisting of many thousand proglottids. These may readily be recognized by the convoluted uterus, and by the openings of the reproductive organs on the median line of one of the flat surfaces, while the head is characterized by being flattened, and provided on the margin with two elongated suckers. The ova give rise to a ciliated larva which becomes transformed into the six-hooked embryo, this latter making its way into the tissues of certain fish, which serve as the first host. Man becomes infected with the worm by eating improperly cooked or salted fish, the Pike being the more usual primary host, though this part may also be played by other forms.

The genus *Tænia* furnishes two human parasites. The genus is characterized by the head being provided with four circular suckers, as well as in some cases with one or more crowns of hooks; the genital pore is situated upon the margin of the proglottids, and the uterus is a straight tube with a varying number of lateral transverse pouches.

Tænia saginata, also known as *T. mediocanellata*, is by far the most frequent tapeworm of man, and may reach a length of 7–8 metres, and consist of 1200–1300 proglottides. The head has no rostellum or crown of hooks, and the proglottids are recognizable by their size, measuring 5–7 mm. in breadth and 18–20 mm. in length, and also by the lateral branches of the uterus being slender and 20 or 30 in number. The Cysticercus occurs in the muscles or occasionally in other organs of cattle, improperly cooked beef being the source of infection for man.

Tænia solium is of less frequent occurrence than *T. saginata*, from which it is easily distinguished by its shorter length, 2–3½ metres, and by the smaller number of proglottids, 800–900. The head, in addition to the four suckers, is provided with a rostellum bearing a double crown of from 26–28 hooks. The proglottids are about 5 mm. broad and 10–12 mm. long, and the uterus has 7–9 stout lateral pouches. The *Cysticercus* state of this worm occurs in the muscles of pigs, whence man becomes infected by eating improperly cooked or salted pork. It measures 8–10 mm., and possesses when imbedded in the muscles an elliptical shape, its long axis being parallel with the long axis of the muscle-fibres. In addition to its occurrence in swine muscle, however, it has also been found occasionally in man, encysted in the muscles, brain, or eye. The source of infection of man is, in many cases at least, cress, lettuce, and such articles of food which have been watered with liquid manure containing the fertilized ova of the worm. The six-hooked embryo which developes from the ovum migrates to the tissues named where it encysts itself, and man becomes the intermediate host of the worm.

In addition to being occasionally the intermediate host of *T. solium*, man may also be the host of the Echinococcus of *T. echinococcus*, a small worm about 4 mm. in length and with only three proglottids, which occurs in its adult state in the intestine of the dog. The ova may be received into the human digestive tract by fondling, and especially by kissing, infected pet dogs, and the six-hooked embryo makes its way to the liver, lungs, brain, or other organs, where it becomes encysted, producing tumors which, especially in the liver, may reach a great size and a weight of from 10 to, in some cases, 15 kilogrammes.

Domestic animals are also apt to be infected with Cestodes in addition to those already mentioned, occasionally with fatal results. This is especially the case with sheep, in whose intestine *T. expansa* may develop in such numbers as to occlude the lumen, and cause death, especially in young lambs. A Cœnurus also occurs occasionally encysted in the brain of sheep, producing a disease known from its symptoms as the "staggers," which may likewise result fatally.

The Relationships of the Cestodes.—In considering the affinities of the Cestoda, the nature of the strobila, so far as its individuality is concerned, must be inquired into. Two views upon this point are open. The older one regards the Cestode as a colony, considering each proglottid an individual equivalent to the scolex, and the process of strobilation one of reproduction by budding. On this view the strobila is exactly comparable to the Scyphostoma strobila, the scolex corresponding to the Scyphostoma base and the proglottids to the Ephyræ. There is undoubtedly much to be said in favor of such a view which regards the reproduction of the Cestoda as a process of alternation of generations, but at the same time it must be recognized that the buds or proglottids are not reduplications of the parent bud as is the case with *Microstoma*, where the budding individual has the adult form. In the Scyphostoma strobila the buds do differ from the parent which gives rise to them; but the Scyphostoma is a larva which gives rise by budding to the adult form, and is comparable rather to the Cysticercus than to the scolex of the Cestode. Non-strobilating Scyphostomas become medusæ, but the scolex never becomes a proglottid, and the latter cannot be considered the terminal stage of the life-history in the same sense as a medusa is. The nervous system of the entire Cestode strobila centres in the brain of the scolex, the various proglottids never developing independent brains, the reproductive organs being practically the only organs which are reduplicated in successive buds.

According to the second view the strobila is an individual, and the strobilation is regarded as a culmination of the reduplication of organs seen in many forms, but more especially in the Nemerteans (q.v.). This view receives strong support from the occurrence of such forms as *Caryophyllæus*, *Ligula*, and *Triænophorus*, described on a preceding page, in which may be seen successive gradations of strobilation, beginning with a simple reduplication of the reproductive apparatus in *Ligula*, this reduplication being accompanied in *Triænophorus* by a tendency for the body to constrict into parts, each of which contains one of the sets of reproductive organs.

The choice between these two views hinges upon the question of individuality. The individuality of either *Ligula* or *Triænophorus* can hardly be questioned, and there is no reason for regarding a *Tænia* for instance as an individual belonging to a higher grade than either of these—a view which the first and older theory implies, since it regards a *Tænia* as a colony of equivalent individuals. Such a form as *Caryophyllæus* is an aggregate of individualities of a lower grade, organ-individuals; and just as the cell-individuals composing these may divide, so the organs, or rather the embryonic masses of cells destined to give rise to them, may bud, producing a reduplication of organs. This reduplication may occur in one or more organs; in the Acœla among the Turbellaria it affects only the testes, in the Alloiocœla it affects both ovaries (the vitellaria being originally parts of the embryonic mass which gives rise to the ovaries) and testes, and in the Rhabdocœla it affects only the ovaries. In the Cestodes the entire reproductive apparatus is reduplicated in this manner, a series being produced, and secondarily a tendency for each member of the series to be capable of separation from its fellows has come about owing to the greater certainty it gives for the perpetuation of the species. A certain amount of individuality of the proglottids is thus brought about, but at the same time the process of strobilation cannot accurately be termed a process of non-sexual reproduction by budding, since the proglottid individuals are not quite of the same grade of morphological individuality as *Caryophyllæus*, which the scolex represents. Both views are correct to a certain extent: the strobilation is a budding off of individuals from the scolex, but of individuals of a lower grade; and the entire strobila is in reality an individual comparable to *Caryophyllæus* or a Trematode.

Considering, then, the strobila as a metamere-individual, what are the affinities of the Cestodes? They seem to have been derived from Trematodes, the simpler forms without reduplication of the reproductive organs being capable of being regarded either as Trematodes without a digestive tract or as Cestodes without any indications of strobilation. If this be true, indications of their affinity should appear in the life-history in accordance with the biogenetic law. One interesting form deserves mention in this respect—*Archigetes*, which occurs in certain Annelids. It is a Cestode without reduplication of organs and provided with a tail, similar in a general way to that of a Cercaria. Certain facts in its life-history seem to indicate that *Archigetes* is comparable, not to an adult Cestode, but to a Cysticercus which has become sexually mature, and it might be expected that similarities to the Trematode Cercaria might be found in Cysticerci. Recently such similarities have been shown to exist in certain Cysticercoids: a tail-like appendage, which later separates and degenerates, has been described as occurring at this stage of the development; and furthermore it has been suggested that the cavity of the Cysticercoid into which the head is invaginated may be equivalent to the Trematode intestine, later on becoming obliterated by the growth of the parenchyma. The evidence at present available points, then, to a derivation of the Cestode from the Trematodes, and from Trematodes in which the Cercaria-stage had already been established.

IV. Class **Nemertina.**

The three preceding classes show marked evidences of genetic affinity, the characteristic differences of structure in the Trematodes and Cestodes being due to the parasitic habits of these forms. The Nemerteans, on the other hand, though apparently tracing descent from a Turbellarian-like ancestor, show a marked advance in structure, and must be regarded as organisms of a considerably higher grade than the other Platyhelminths.

They are for the most part marine, though a few forms inhabit fresh water or even damp earth, and are usually elongated ribbon-like forms, reaching a length, in some cases, of several centimetres. The body is externally unsegmented, though a more or less marked metamerism of the internal organs, due to their repetition at definite intervals, may be present. The ectoderm of the body resembles that of the Turbellaria in being throughout ciliated, and rests upon a basement membrane, which in some cases contains cells. Within the membrane are a varying number of muscle layers, differentiations of the outermost portions of the mesodermal tissue, which in the form of a parenchyma occupies the interval between them and the digestive tract. This (Fig. 84, *d*) is an almost straight tube, except in the genus *Malacobdella*, and is pushed out on each side into sac-like pouches, which are arranged in some cases with a regularity of succession almost metameric. It opens to the exterior at the anterior end of the body by the mouth, a short non-muscular œsophagus intervening between the intestine proper and that opening; and at the other end of the body is a second communication with

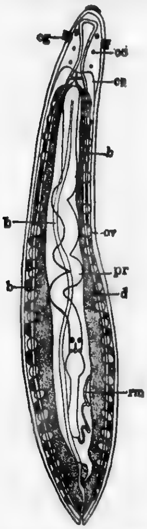

Fig. 84.—Stichostemma Eilhardi (after Montgomery).

b = blood-vessels.
ce = cerebral ganglion.
cg = ciliated funnel.
d = intestine.
oc = eyes.
ov = ovary.
pr = proboscis.
rm = retractor muscle.

the exterior, the *anus,* an opening unrepresented in other Platyhelminths. The digestive tract is no longer a blind sac, but has the form of a tube, as in all the higher types.

In the anterior end of the body, above the digestive tract, is a structure, the *proboscis* (Fig. 84, *pr*), essentially peculiar to the Nemerteans, although indications of such an organ are to be found in the *Rhabdocœla.* It consists of a closed tube, the *proboscis sheath,* with muscular walls, imbedded in the body parenchyma and extending backwards in some cases almost to the end of the body, and within it lies the proboscis, also a tube, united to the wall of the sheath near its anterior end and in fact closing it at that region. From this line of attachment the proboscis stretches back in the cavity of the sheath, the space between it and the walls of the sheath being filled with fluid. It is a simple invagination into the cavity of the sheath of the external body-wall, whose musculature as well as ectoderm are continuous with that of the proboscis. From the tip of the invagination a band of muscle fibres, forming the *retractor muscle* (*rm*) of the proboscis, passes to the wall of the body. By the contraction of the muscular walls of the sheath the fluid contained in its cavity forces the proboscis to be evaginated sometimes with sufficient force to tear itself loose from its line of attachment; but should this accident not happen, the proboscis can be reinvaginated by the contraction of its retractor muscle. The function of this organ is doubtful. In some cases it is undoubtedly a weapon of offence and defence; but it seems not improbable, from its rich nerve-supply and from the probable function of its prototype in the Rhabdocœla, that in some cases at least it may be a tactile organ.

A well-developed nervous system is always present, though it may show in some cases, as *Carinella,* the primitive character of being still imbedded in the ectoderm or else lying immediately beneath it. In other cases, however, as *Cerebratulus,* it is enclosed in the muscles of the body-wall or may even be completely within them, imbedded in the parenchyma. It consists in its most usual form of two ganglionic masses (Fig. 84, *ce*) from which short nerves pass forwards and which are united by two transverse commissures, one of which passes over or in front of the œsophagus, while the other arches from one ganglionic mass to the other over the proboscis sheath. Each ganglion is bilobed, the smaller posterior lobe being in some cases united to the larger one by a relatively thin band of nerve-tissue so that it appears to be almost independent. From the larger lobe of each side a nerve-cord passes towards the posterior end of the body, where the two may unite to form an arch passing over the posterior part of the intestine. In addition to these a third nerve originating from the commissure passing over the proboscis sheath and running backwards in the median dorsal line is frequently present as well as, in some forms, another nerve running along the dorsal wall of the proboscis sheath, to which it sends branches. In many forms, such as *Cerebratulus*, a fine plexus of nerve-tissue, lying between the muscle layers of the body-wall, unites the three main nerve-cords, some of the strands of the plexus being sometimes larger than the others and forming circular commissures between the nerve-cords; in *Tetrastemma* and *Amphiporus*, for example, these circular commissures may be strongly developed and have an almost metameric arrangement, the general plexus being in such cases wanting.

Eyes (Fig. 84, *oc*) are present in some forms occasionally in considerable numbers, but are frequently wanting, and otocysts occur but seldom. The lateral ciliated grooves which occur on the sides of the head of some Rhabdocœla reach in the Nemerteans a high development (*cg*), in some forms, e.g. *Cerebratulus* and *Tetrastemma*, becoming ciliated funnels of some length, whose inner ends are imbedded in the substance of the posterior lobe of the brain. An olfactory function has been assigned to these organs, though some authors have considered them mainly respiratory.

The excretory system consists of a longitudinal canal on each side in the anterior portion of the body, sometimes replaced by a network of canals, which opens to the exterior by one or more ducts leading to pores situated on the margin of the body. In some cases these lateral ducts and the pores may be quite numerous and, like the intestinal pouches and the circular nerve-commissures, may have a somewhat metameric arrangement. The various terminal branches of the nephridial tubes are club-shaped and closed, a flame of cilia projecting from the closed end into the lumen of the tube. The canals and tubes are lined with ciliated cells, and are therefore intercellular and not intracellular, i.e., do not perforate cells, differing in this respect from the nephridia of other Platyhelminths.

The blood-vascular system is peculiar to the Nemertea among Platyhelminths, and consists in the simple forms, such as *Carinella*, of two lateral vessels which anteriorly open into lacunar spaces without definite walls. In the more highly organized forms, however, three longitudinal trunks, two lateral and one dorso-median, are present with definite and sometimes muscular walls, and unite in a ⊥-shaped manner at the posterior end of the body, while in front they may either open into a system of lacunæ, or they may, as in *Stichostemma*, unite with each other, a perfectly closed system thus resulting (Fig. 85, *b*). Transverse connecting branches between the dorsal and lateral vessels occur in regular succession, a metamerism being again suggested. The blood-vessels and lacunæ contain a fluid in which float round or elliptical corpuscles, which in some of the higher forms have a red color, due to the presence of hæmoglobin. No heart or special contractile organ is present, the blood being driven through the vessels, without any definite direction, by the movements of the body.

The occurrence of a blood-vascular system in the Nemerteans and its character in the lowest members of the group suggests a mode of origin for the system which agrees well with what may be deduced from embryological observations on other forms. It may be supposed that in the primitive Nemerteans a system of spaces filled with fluid existed, in which cells derived from the parenchyma floated. These spaces would represent a simple cœlom, and were lacunar in character, lacking definite walls, the circulation of the fluid they contained being very irregular. In time the spaces along the sides of the body might arrange themselves in a linear manner, and might acquire definite walls, the rest of the spaces remaining lacunar, when a condition resembling that in *Carinella* would ensue, the arrangement found in higher forms resulting from the conversion of the remaining lacunar spaces into vessels with definite walls.

According to this view the blood-vascular system is to be regarded as in reality a portion of the cœlom separated off for a special purpose, and other instances bearing the same significance will be noticed later.

The reproductive system differs from that of the other Platyhelminths in its much greater simplicity, no vitellaria or shell-gland being present, and furthermore the Nemerteans are almost without exception of separate sexes. The ovaries (Fig. 84, *ov*) or testes are present in considerable numbers, one lying in each interval between two lateral diverticula of the intestine, so that they partake in their arrangement of the more or less pronounced metamerism of that organ. Between the intestine and the genital masses there is in some forms a distinct cavity, or cœlomic space, and at the time of maturity a separate communication with the exterior forms for each ovary or testis.

The class Nemertina may be divided into four orders, whose chief characteristics may be briefly stated, having been for the most part already described.

1. Order **Palæonemertini.**

To this order belong the genus *Carinella* and allied forms, all characterized by structural peculiarities which are to be regarded as primitive. The lateral ciliated organs are, as in the Rhabdocœla, mere grooves, not being continued inwards to the brain in the form of a funnel; and furthermore the nervous system is either imbedded in the ectoderm or lies immediately below it. To these characters may be added the more or less lacunar nature of the blood vascular system, and the communication, in some cases, of the nephridia with it.

2. Order **Schizonemertini.**

In the Schizonemertini the ciliated funnels are well developed, and the nervous system is imbedded in the muscular layers of the body-wall; and though the nerve-cords are still, as in the preceding order, united by a plexus, nevertheless there are indications of a development of commissural connecting nerves. The blood vascular system is still lacunar anteriorly, though posteriorly three well-defined vessels are present. The genus *Cerebratulus* belongs here.

3. Order **Hoplonemertini.**

This order, which includes the genera *Tetrastemma* and *Amphiporus* mentioned above, has, like the preceding order, ciliated funnels as lateral organs, and the nervous system lies completely within the muscular layer of the body-wall and the nerve-cords are united by transverse commissures, the plexus being wanting. The blood vascular system is a closed series of tubes, not communicating with lacunar spaces. The most striking characteristic of the order is, however, the structure of the proboscis, which is armed near its posterior (that is, while invaginated) end by one or more dagger-like spines or stylets. The most posterior portion is not capable of being evaginated, and its walls are glandular, secreting a poisonous fluid which is poured into the more anterior portion of the tube, bathing the stylets and thus being carried into the wound which may be made by the forcibly evaginated proboscis with the stylets coming into contact with the body of the prey or enemy.

4. Order **Malacobdellina.**

This order contains a single genus, *Malacobdella*, which is found in the mantle-cavity of marine Lamellibranchs, such as the common Mussel and Clam. It resembles the *Hoplonemertini* in many particulars, but is destitute of lateral ciliated organs, and its proboscis possesses no stylets. The intestine is a convoluted tube without lateral diverticula, and the hind end of the body is provided with a sucker.

Development of the Nemertina.—In some Nemerteans, such as *Tetrastemma* and *Malacobdella*, the young worm leaves the egg in the form of a cylindrical ciliated larva, usually provided at the extremities of the body with bunches of longer cilia, which may possibly be sensory in function, and gradually changes without any marked metamorphosis into the adult form. The mouth opens upon the ventral surface of the body into a retort-shaped digestive tract which in early stages possesses no anus—this structure only appearing much later. In many forms, however, a peculiar metamorphosis occurs during the transformation of the larva, known from its first describer as *Desor's larva*, into the adult. On the ventral surface of the body there appear four invaginations of the ectoderm, two situated in front of the mouth and two behind it, which gradually separate from the ectoderm to form four single-layered plates lying immediately beneath it. By a subsequent growth and fusion of these plates a new ectodermal covering is formed enclosing the internal organs, and on its completion the original larval ectoderm is thrown off. In some species a somewhat more complicated process occurs. The larva, known as the *Pilidium* (Fig. 85), has the shape of a helmet from whose rim two ear-like lappets hang down, between which lies the mouth-opening (*m*), while at the apex of the helmet there is an ectodermal thickening (*ap*), nervous in character, from which projects a bunch of strong sensory cilia. As in the Desor larva four invaginations of the ectoderm of the ventral surface occur, which, however, separate from the larval ectoderm as four hollow sacs which unite together, their inner walls thickening to form the ectoderm of the young Nemertean, while the outer walls become thin and form what is termed the *amnion* surrounding a cavity within which lies the young worm. During the process of fusion of the four sacs the enteron (*S*) and a portion of the mesoderm of the *Pilidium* are enclosed and give rise to the digestive tract and mesoderm of the young worm, which later breaks through the amnion and Pilidium wall to become free.

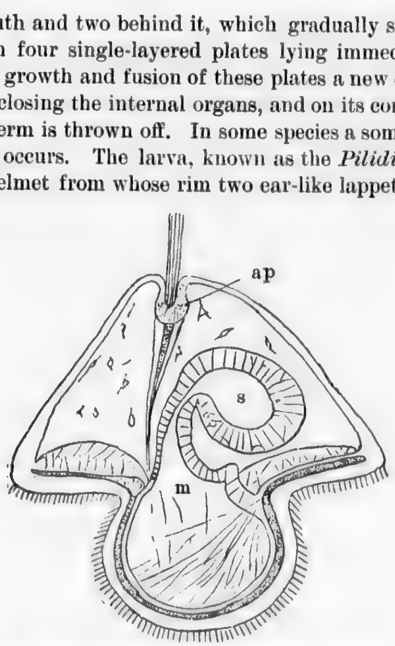

FIG. 85.—*Pilidium* LARVA (after SALENSKY).

ap = apical plate. *m* = mouth. *s* = digestive sac.

The significance of this metamorphosis is decidedly obscure. Some authors regard it as more primitive than the direct method of development, on the ground that the *Pilidium* with its lappets presents general similarities to the Müllerian larva of the Polyclades and is derived phylogenetically from such a form, being therefore more ancestral in its characters than the simpler larvæ. It must be recognized, however, that there is no indication of metamorphosis in the Polyclad larvæ, and furthermore that the Nemerteans perhaps show greater similarities to Alloiocœlan Turbellaria than to Polyclads. Perhaps an explanation of the process is to be found in the sloughing of the ectoderm and the formation of new ciliated cells which is seen in the larva of a Palæonemertean, *Cephalothrix*, the metamorphosis of Desor's larva and of the *Pilidium* being a greater and more complicated ecdysis derived from the simpler one.

Some interesting evidence as to the morphological significance of the anus is to be derived from a study of its development in the Nemerteans. It is an opening which has been considered by some to have arisen by the closure in the middle of an elongated slit-like blastopore—the two ends, however, remaining open to form respectively the mouth and anus; and it has been thought that the direct transformation of the blastopore into the permanent mouth in some cases, and in others into the permanent anus, receives on this theory an explanation. The phenomenon of the closure of the blastopore in the middle does actually occur in the Annelid-like Tracheate *Peripatus*, and in many forms both mouth and anus stand in close ontogenetic relationship to the blastopore. In the Nemerteans are represented the most lowly organized animals which possess both mouth and anus, and accordingly it might be expected that in them the original relationships will be most clearly seen. The young Nemertean possesses no anus. It resembles, so far as its digestive tract is concerned, an Alloiocœlan; it is only relatively very late in its life-history that the anus appears, and then in a region of the body which has no relation whatever to the original blastopore. This fact should carry considerable weight with it, especially as in the majority of forms the anus is, in comparison with the mouth, of relatively late formation. It seems not improbable that primitively it had no relation with the blastopore, and where such relations do occur they are entirely secondary.

The indication of metamerism seen in the Nemerteans needs no further discussion after what has been said on p. 48 with reference to similar peculiarities in the Turbellarians.

SUBKINGDOM METAZOA.

TYPE PLATYHELMINTHES.

I. Class **Turbellaria.**—Ectoderm ciliated; no anal opening.
  1. Order *Acœla.*—Mouth present, but no digestive tract. *Convoluta.*
  2. Order *Alloiocœla.*—Digestive tract present; space between it and body-wall occupied by parenchyma. *Monotus, Plagiostoma.*
  3. Order *Rhabdocœla.*—Digestive tract straight rod- or sac-like; space between it and body-wall not filled with parenchyma. *Microstoma, Mesostoma, Prorhynchus, Vortex.*
  4. Order *Tricladea.*—Digestive tract branched, three principal limbs giving rise to secondary branches: male and female reproductive

organs with common opening. *Gunda*, *Planaria*, *Phagocata*, *Dendrocœlum*, *Bdelloura*, *Bipalium*, *Syncœlidium*.

5. Order *Polycladea.*—Digestive tract branched, the primary branches being numerous; male and female organs having separate openings.

   (*a*) With terminal sucker (*Cotylea*). *Thysanozoon*, *Eurylepta*.

   (*b*) Without sucker (*Acotylea*). *Planocera*, *Leptoplana*, *Stylochus*.

II. Class TREMATODA.—Ecto- or endoparasites; ectoderm not ciliated; with digestive tract and suckers.

1. Order *Polystomeæ.*—Suckers more than two; development direct; usually ectoparasites. *Polystomum*, *Sphyranura*, *Tristomum*, *Gyrodactylus*.

2. Order *Distomeæ.*—Suckers one or two; development indirect; usually endoparasitic. *Distomum*, *Monostomum*.

III. Class CESTODA.—Endoparasites; ectoderm without cilia; no digestive tract or mouth; usually strobilated. *Tænia*, *Bothriocephalus*, *Caryophyllæus*, *Ligula*, *Triænophorus*, *Archigetes*.

IV. Class NEMERTINA.—Ectoderm ciliated; not parasitic; anus present; with protrusible proboscis.

1. Order *Palæonemertini.*—Lateral ciliated funnels shallow; nervous system imbedded in ectoderm; proboscis without stylets. *Carinella*.

2. Order *Schizonemertini.*—Lateral ciliated funnels deep; nervous system imbedded in muscle-layer; proboscis without stylets. *Cerebratulus*.

3. Order *Hoplonemertini.*—Lateral ciliated funnels deep; nervous system within muscle-layer; proboscis with stylets. *Tetrastemma*, *Amphiporus*.

4. Order *Malacobdellina.*—No lateral ciliated funnels; proboscis without stylets. *Malacobdella*.

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CHAPTER VIII.

TYPE NEMATHELMINTHES.

THE Nemathelminths are, like the members of the preceding type, characterized by the form of the body, which is cylindrical and usually elongated or even thread-like, whence the popular terms Round-worms or Thread-worms which are frequently applied to them. The ectoderm is covered by a thick layer of cuticle which it secretes, and in connection with which spines, bristles, or hooks may be developed at various parts of the body. There is no trace of segmentation or reduplication of organs, with the exception that in some forms the circular nerve-commissures uniting the longitudinal cords may succeed each other with tolerable regularity; the cuticle, it is true, especially when thick, is ringed by numerous grooves succeeding one another at short intervals, but this cannot be interpreted as an indication of metamerism, but is more probably a provision to counteract the rigidity of the cuticle and to give a considerable amount of mobility to the body. The Nemathelminths accordingly have the same grade of individuality as a simple Platyhelminth, such as an Alloiocœlan, and are to be regarded as metamere individuals.

One important difference of structure which these worms show from the Platyhelminths is the presence of a capacious cœlom, the interval between the digestive tract and the musculature of the body-wall not being filled up by parenchymatous mesoderm, but being a simple undivided cavity in which lie the reproductive organs. These latter are simple, the animals being as a rule bisexual, and there is no separation of the female organ into ovary and vitellarium. Structures of an excretory nature occur in one of the two classes into which the type is divisible, but a blood vascular system is entirely wanting.

The habit of life varies greatly in the various members of the group. In the class Nematoda many forms live freely in the sea, fresh water, or damp earth, while others are parasitic during a part of their lives, and others again are parasites practically throughout their whole existence. The Acanthocephala are without exception parasitic.

I. Class **Nematoda.**

The Nematodes are distinguished from the members of the second class by the presence in nearly all cases of a distinct digestive tract, usually with mouth and anus, and by the absence of a retractile proboscis furnished with hooks at the anterior end of the body. The arrangement of the muscles of the body-wall are also peculiar inasmuch as longitudinal muscles only are present (Fig. 86, *m*), which instead of forming a closed sheath are interrupted along four longitudinal lines (*d*, *v* and *s*), or in some cases along a single ventral line, in the former case there being four longitudinal bundles of muscles extending the length of the body. In the structure of most of the organs, however, considerable variation is found, and it will be most convenient to describe them as

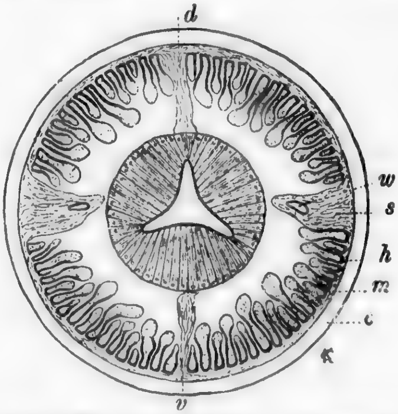


Fig. 86.—Transverse Section of *Ascaris lumbricoides* at the Level of Pharynx (from Hertwig).

c = cuticle.
m = longitudinal muscles.
d = dorsal line.
s = lateral line.
h = hypodermis.
v = ventral line.
w = nephridium.

they are found in each of the two orders into which the class may be divided.

1. Order **Eunematoda.**

This order contains the majority of the Nematoda, and all its members are furnished with a mouth and anus and a functional digestive tract. The mouth is in some cases at the bottom of a funnel-like depression which may be armed with spines, special developments of the cuticula which covers the body. This is throughout cylindrical in shape, except that in the males of some species it expands at the posterior extremity into a relatively large funnel-shaped structure with thin walls, the *bursa* (Fig. 87), at the bottom of which lies the opening of the cloaca, a cavity into which the intestine and the male reproductive organ open. Beneath the ringed cuticle lies the ectoderm (*hypodermis*) which secretes it, and beneath this the muscular layer which consists only of longitudinal muscle-fibres, differentiations of the outer ends of large cells whose undifferentiated inner ends project into the cœlom, so as almost to obliterate it in some cases. The muscle-fibres do not, however, form a complete continuous sheath surrounding the cœlom, but are interrupted along four longitudinal lines, two lateral, one dorsal, and one ventral (Fig. 86). The cœlom contains the intestine and reproductive organs, and is peculiar in that it is not bounded by a limiting cellular membrane or peritoneal lining, being simply a space comparable to the cœlomic cavities of the Rhabdocœla or the blood-sinuses of the Nemerteans.

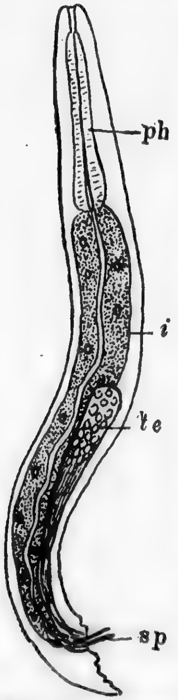


Fig. 87. — *Ascaris nigrovenosa* Male (after Leuckart).
i = intestine.
ph = pharynx.
sp = spicules.
te = testis.

The digestive tract is a straight tube traversing the body from one extremity to the other, opening posteriorly in the female directly to the exterior, in the males into a *cloaca* common to it and to the male organ of reproduction. Its anterior part is a muscular œsophagus lined with cuticle directly continuous with that covering the surface of the body, while posteriorly it is a delicate tube composed of a single layer of cells, not being surrounded by any mesodermal muscular tissue.

The excretory system is not as yet fully understood. It appears to consist of a pair of tubes, for which no cellular lining has as yet been made out, which lie, one on each side, in the thickened hypodermis of the lateral lines. In the anterior portion of the body they unite to form a single tube which opens to the exterior in the median ventral line not far behind the brain (Fig. 88, B).

This latter consists of a ring or nerve-collar surrounding the anterior part of the œsophagus on which lateral masses of ganglion-cells occur and which gives rise to two main nerves, one of which runs back in the median dorsal line, while the other, which in some forms appears to be double, lies in the median ventral line. Other nerves pass forwards from the nerve-ring to the anterior part of the body, and in addition to the dorsal and ventral nerve-cords two lateral nerves pass backwards a short distance, while circular commissures connect the two main nerve-cords, those of the two sides of the body not, however, being opposite each other, so that they do not suggest a pseudo-metamerism so strongly as the similar commissures of the Hoplonemertini. Special sense-organs are as a rule absent, though a few forms possess eyes.

The reproductive organs are exceedingly simple. In the male they are represented by a single convoluted tube, lined in its upper part by the mother-cells of the spermatozoa and dilating below into a seminal vesicle, to which succeeds a short ejaculatory duct which opens into the cloaca. The walls of this latter cavity are frequently invaginated to form two small sacs in each of which lies a chitinous spicule capable of being protruded from the cloacal opening and serving, with the bursa, as copulatory organs. The female organs, on the other hand, consist of a pair of convoluted tubes, each of which dilates into a uterus and unites with its fellow to form a single tube, the *vagina*, sometimes with muscular walls, which opens to the exterior in the ventral mid-line some distance in front of the anus. As a rule the sexes are separate, hermaphroditism occurring only in a few isolated cases.

Many Nematodes are free throughout their entire existence, living in the sea, fresh water, or damp earth, and frequently possessing eyes. Others are found in some domestic products, such as the vinegar-eel (*Anguillula*), found in vinegar and sour paste; while others, again, are parasitic on plants, such as *Tylenchus*, which lives upon the young grains of wheat and in some cases produces very serious damage to crops, and *Heterodera*, which is quite as injurious to root-crops. More interesting, however, are a number of forms occurring as parasites in animals, many affecting man, in some cases producing serious results.

Life-histories of the Eunematoda.—The free-living forms show no peculiarities of development, the immature animal developing directly from the egg. Among the parasitic forms, however, interesting variations from direct development, due to a change of host, occur, a well-marked heterogony occasionally being found. An example of this is seen in *Rhabditis nigrovenosa*, which at one stage of its existence lives in damp earth, the females being viviparous and producing young which make their way into the lungs of frogs, where they assume a form which led them to be assigned to the genus *Ascaris*, and where they become mature. At this stage they differ from the *Rhabditis* forms in being hermaphrodites, and from the eggs deposited by them the Rhabditis generation again results.

From a medical standpoint one of the most important forms is *Trichina spiralis*, which occurs encapsuled in the muscles of various warm-blooded animals, such as man, the pig, rat, mouse, and occasionally in the fox, cat, and rabbit. The capsules are oval and about 0.6 mm. in length, and occasionally have a white color, due to the deposition of calcareous matter in the wall. In the interior of the capsule lies coiled up an immature *Trichina*, which may retain its vitality in this condition apparently during the lifetime of its host. Should, for instance, improperly cooked or salted pork which contains such capsules be eaten by man, the capsule becomes dissolved by the digestive juices and the young *Trichina* is set free in the small intestine and in the course of a few days becomes sexually mature.

The males die shortly after having reached maturity, but the females bore into the intestinal walls, some passing through into the mesentery, where they may continue to exist for several weeks. They are viviparous and each individual may produce as many as 10,000 young, which make their way to the voluntary muscles, especially to those of the neck and to the diaphragm, partly by the lymphatic and blood vessels, and partly by active migration in the connective tissue. The young *Trichinæ* measure about 0.01 mm., and during their passage into the substance of the muscles they produce more or less severe inflammatory disturbances. Having reached the muscle tissue they become encysted therein (Fig. 89, A), the cysts measuring about 0.4 mm. in length, and if the disturbances which they produce have not proved fatal to the host the danger is past, the encapsuled *Trichinæ* undergoing no further development within this host, though they may retain their vitality for many years.

Other forms which occur in man are *Ascaris lumbricoides*, the round-worm (Fig. 88, B), a large form, of which the female measures 40 cm. in length and the male 25 cm., and which bears some resemblance in shape to an earth-worm, *Oxyuris vermicularis*, a smaller form, 1 cm. in length, which inhabits the rectum especially of young children, and *Trichocephalus dispar* (Fig. 88), which measures 3–5 cm. in length and is characterized by the anterior half of the body being exceedingly slender, the worm boring into the intestinal wall, especially in the neighborhood of the cæcum, by this slender portion, the hinder thicker portion hanging freely in the wall of the intestine. The presence of these three forms may be recognized, independently of the finding of the actual worm, by their ova, whose respective characters differ very greatly. So far as is known the development of these forms is direct and there is no intermediate host, but the ova are taken into the body with the food. Personal uncleanliness and imperfect drinking-water may be causes of infection.

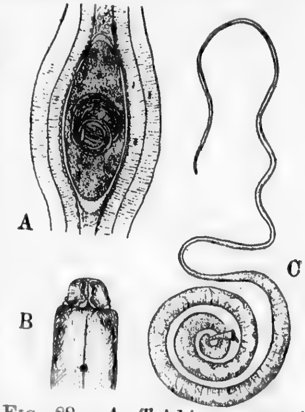
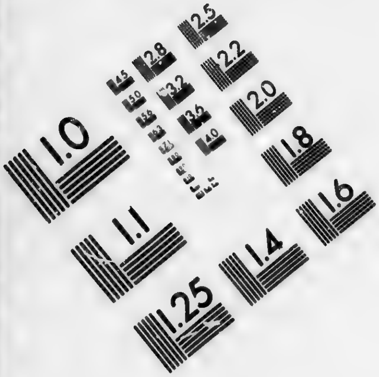
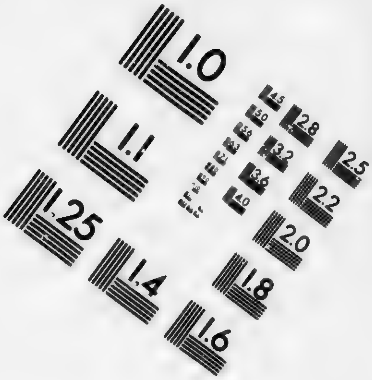


FIG. 88.—*A*, *Trichina* encysted in muscle; *B*, anterior extremity of *Ascaris lumbricoides* from the ventral surface, showing the two ventral oral papillæ and the excretory pore (both after LEUCKART); *C*, *Trichocephalus dispar* (after OWEN).

In addition to the forms which have been mentioned there are a few which are more especially frequent in tropical climates. *Dochmius duodenalis* is a small form about 1–2 cm. in length, with strong teeth or blunt spines in the mouth region, which fastens itself to the wall of the small intestine and lives upon the blood of its host, producing anæmia. Its ova develop in stagnant water or damp earth, and probably man becomes directly infected. It has long been known in the tropics, producing the disease known as *Chlorosis ægyptiaca*, but may also affect miners or workers in tunnels, having appeared endemically in the workers on the St Gothard tunnel, whence it has since spread somewhat in Germany, especially among workers in clay. *Filaria medinensis* is limited entirely to the tropics and is a very slender worm nearly 1 metre in length which lives in the connec-





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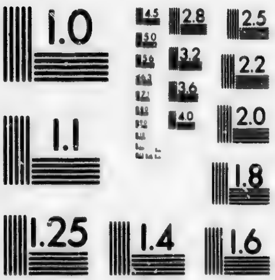
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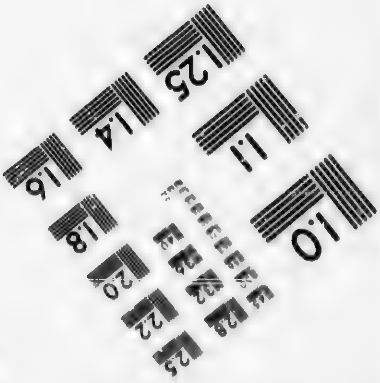

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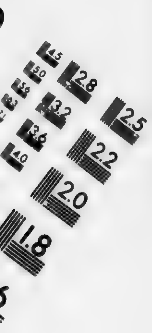
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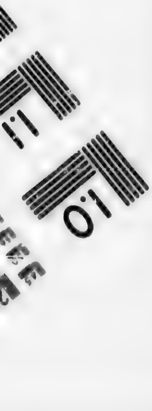
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tive tissue beneath the skin, producing ulcers, at the bottom of which the worm lies coiled up. The ova develop in water and the embryos pass probably into small Crustacea, which are swallowed with drinking-water. *Filaria sanguinis hominis*, also solely tropical in its distribution, receives its name from the fact that it lays its ova in the blood of man, which may thus swarm with countless numbers of small worms. These make their way to the exterior of the body by the kidneys, producing hæmorrhages or minute abscesses in that organ and, as the result of these, milky or bloody urine.

2. Order **Gordiacea.**

This order includes the families of the *Gordiidæ* and *Mermithidæ*, long slender thread-like worms, which differ from the Eunematoda in several important respects. They occur in their mature state in fresh water; in their immature stages, however, they are parasitic in insects. In the adult *Gordius* the mouth is usually closed by an overgrowth of the cuticle, and the anus is lacking in *Mermis*. The musculature of the body-wall consists only of longitudinal fibres (Fig. 89, *m*), which differ in their arrangement from those of the Eunematoda in being interrupted only in the mid-ventral line. The cœlom is lined by a peritoneal epithelium (*p*) lying beneath the

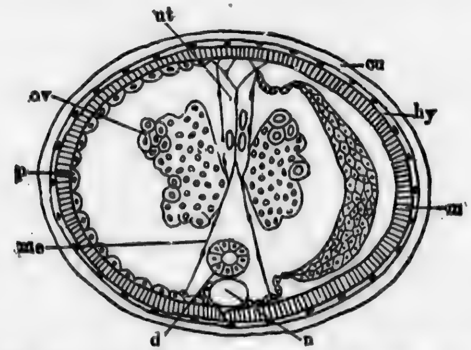

FIG. 89.—TRANSVERSE SECTION OF *Gordius* (after VEJDOVSKY).

cu = cuticle.
d = intestine.
hy = hypodermis.
m = longitudinal muscles.
me = mesentery.
n = nerve-cord.
p = peritoneum.
ut = uterus.
ov = oviduct.

muscle-cells, and is divided into two lateral chambers by a *mesentery* (*me*) running the entire length of the body and consisting of two layers surrounding the intestine (*d*), and inserted into the body-wall dorsally and ventrally, their outer surfaces being lined by a continuation upon them of the peritoneal epithelium.

No excretory system has been as yet discovered. The nervous system consists of a ganglionic ring surrounding the œsophagus, from which a number of nerves pass forward, while a single nerve-cord (*n*) passes backwards in the mid-ventral line, dilating at the posterior end of the body into a ganglionic mass.

The reproductive organs consist in the female of a series of ovaries (*ov*) attached one behind the other to each mesentery above the intestine. In the mesenteries two tubes (*ut*) pass backwards which receive some of the ova and function as uteri, near the hind end of the body bending ventrally to open into the cloaca, whose wall is invaginated to form a single seminal receptacle. The testes have not yet been found, but two seminal vesicles, corresponding to the uteri of the female, occur and open likewise into the cloaca, which in the male is evertible and serves as a copulatory organ.

The Affinities of the Nematodes.—The relationships of the Nematodes are exceedingly obscure. Their unsegmented character and the character of the nervous system seem to ally them more closely with the Platyhelminths than with higher forms, but the relationships to any of the known Platyhelminths must be exceedingly remote. The parasitism which occurs so frequently in the group is to be considered as secondary, since so many forms lead a free life and peculiarities of structure can hardly be attributed to degeneration. The Gordiacea stand on a higher plane than the Eunematoda, as shown by the possession of a mesentery and the arrangement of the reproductive organs and nervous system, which bear some similarities to those of the Annelids, but their Nematode characteristics are most pronounced. Perhaps the ancestors of the Nematodes are to be found in the yet unknown intermediate forms between the Platyhelminths and Annelids, a view which would account for their similarities in certain respects to both these groups.

II. CLASS **ACANTHOCEPHALA.**

This class contains a number of parasitic forms which occur more especially in the digestive tract of fishes, though also found in Mammalia and in exceptional cases in man. A great uniformity of structure exists throughout all the species, so that they are all referable to a single genus, *Echinorhynchus*. The body (Fig. 90) is cylindrical and as a rule not very long, and a marked distinction from the Nematodes is found in the retractile proboscis (*pr*) occurring at the anterior end of the body. It is a cylindrical prolongation of the anterior portion of the body and is provided with a number of chitinous hooks by means of which it adheres to the intestinal wall of its host. The proboscis may be invaginated into a double-walled muscular proboscis-sheath by whose contraction it may again be protruded, a strong retractor muscle, extending from the tip of the proboscis to the base of the sheath, serving for the invagination; and from the base of the sheath retractor muscles (*rm*) pass to the body-walls and serve to hold the sheath in position. No traces of a digestive tract occur.

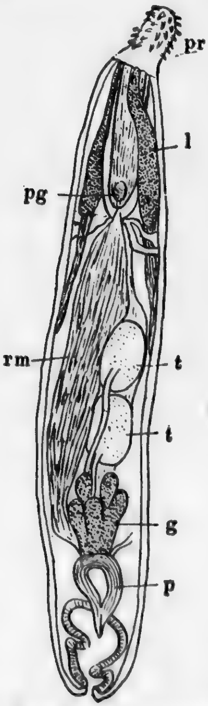

Fig. 90.—Male *Echinorhynchus* (after **Leuckart**).
g = glands.
l = lemniscus
p = penis.
pg = proboscis ganglion.
pr = proboscis.
rm = retractor muscle.
t = testis.

The body is covered upon the outside by a thick cuticle secreted by the subjacent hypodermis, which is a rather thick layer consisting of a protoplasmic matrix in which nuclei are scattered but in which no cell-outlines are to be distinguished. Beneath the cuticle the matrix has a fibrillar character, and near its inner surface it is hollowed out into a network of anastomosing canals of which mention will be made later. Beneath the hypodermis lies a basement-membrane within which are two layers of muscle-cells, having the same epithelio-muscular character as those of the Nematodes, the fibres of the external layer having a circular direction, while those of the inner layer have a longitudinal course. The body-wall encloses a well-marked cœlom, not lined by a special peritoneal epithelium, but which contains the reproductive organs and is traversed by the retractor muscles of the proboscis-sheath.

The nervous system consists of a ganglionic mass (*pg*) lying within the proboscis-sheath which sends forward nerves for the supply of the walls of the sheath and of the retractor muscle of the proboscis. Posteriorly two lateral nerve-cords extend backwards along the sides of the body, and in male individuals are connected near the posterior extremity with a ganglion lying beneath the reproductive ducts and from which nerves pass to the genital apparatus.

The system of lacunar canals which form a network in the lower layers of the hypodermis is probably excretory in function. The canals are found throughout the entire hypodermis, both in the proboscis and in the body-wall, in the latter there being indications of two larger lateral trunks. From the point of junction of the proboscis with the body-wall two muscular sacs, the *lemnisci* (*l*), hang down into the cœlom. The cavity which they contain communicates with a circular lacuna which surrounds the base of the proboscis and with which the lacunæ of the proboscis-hypodermis likewise communicate, this system of the proboscis-lacunæ and the lemnisci being shut off from the system of the body-wall by a partition extending from the basement-membrane to the cuticle. The lemnisci have been regarded as possible representatives of a digestive tract, but it seems more probable that they are reservoirs for the reception of the fluid contained in the lacunæ of the proboscis when it is driven from them during invagination.

The reproductive organs are much more complicated than those of the Nematodes. The sexes are separate, the male individuals being usually smaller than the females. The ovaries are paired bodies enclosed within a muscular *ligament* attached anteriorly to the base of the proboscis-sheath and posteriorly to the reproductive duct. At an early stage of their development, however, the ovaries split up into masses which float about in the cœlom together with large numbers of separated ova. They pass to the exterior by a complicated system of ducts, the most anterior portion of which is a wide funnel-shaped structure, the *bell*, to whose wall the ligament is attached and which, by a rhythmical expansion and contraction, engulfs the ova and ova-masses floating about in the cœlom. From the lower end of the bell they escape, the ova-masses to be returned to the cœlom, while the fertilized separate ova pass into a short tube, the *oviduct*, which opens below into a muscular *uterus*, which finally communicates with the exterior at the posterior end of the body.

The male apparatus consists of usually two testes (Fig. 90, *t*) enclosed within the ligament, which is attached below to the wall of the evertible *bursa*. From each testis a duct passes backwards, the two soon uniting to the single *vas deferens*, which, after receiving the ducts of some unicellular glands (*gl*), opens into the bursa at the tip of a muscular *penis* (*p*). The bursa when everted is a somewhat funnel-shaped structure at the bottom of which is the penis, the edge being furnished in some forms with hooks by means of which it serves as a copulatory organ.

The life-history of the *Acanthocephala* includes a change of host. The larvæ are found in the body-cavity of Crustacea or insects, and reach maturity only when the intermediate hosts are swallowed by the proper final host. The largest species of *Echinorhynchus* is the *E. gigas*, which occurs in the intestine of the pig; the intermediate host of this form is the June bug (*Melolontha*, *Lachnosterna*).

Nothing can as yet be stated with any certainty concerning the relationships of the *Acanthocephala*. They are usually associated with the Nematodes, to which they certainly present similarities, but no intermediate forms bridging the gap between the two classes are yet known, and the embryological history throws little light upon the question.

SUBKINGDOM METAZOA.

TYPE NEMATHELMINTHES.

I. Class NEMATODA.—With digestive tract; without proboscis furnished with chitinous hooks.

1. Order *Eunematoda*.—Musculature of body-wall interrupted along the lateral line; no mesentery; no peritoneal epithelium. *Anguillula*, *Tylenchus*, *Heterodera*, *Trichina*, *Ascaris*, *Oxyuris*, *Trichocephalus*, *Dochmius*, *Filaria*.

2. Order *Gordiacea.*—Musculature of body-wall not interrupted along the lateral line; with mesentery and peritoneal epithelium. *Gordius, Mermis.*

II. Class ACANTHOCEPHALA.—Without digestive tract; with proboscis armed with recurved chitinous hooks; parasitic throughout. *Echinorhynchus.*

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CHAPTER IX.

ORDER ECHINODERA; CLASS CHÆTOGNATHA; CLASS ROTIFERA; ORDER GASTROTRICHA; DINOPHILUS.

THIS chapter includes a description of a number of forms whose affinities are at present rather doubtful and which show similarities sometimes to the Nemathelminths and sometimes to the Annelida. Instead, however, of assigning them to one or the other of these types, it has been thought advisable to consider them in a separate chapter and each group independently, indicating briefly their most probable affinities.

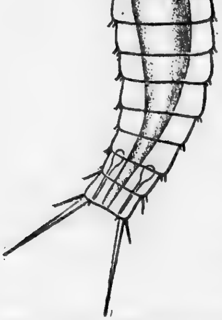

FIG. 91. — *Echinoderes Dujardinii* (after CLAPARÈDE from HATSCHEK).

Order **Echinodera.**

The order Echinodera includes a number of small organisms all marine in habitat, and all referable to a single genus, *Echinoderes* (Fig. 91). The body varies in length from somewhat less than 1 mm. to almost 0.1 mm. according to the species, and tapers somewhat posteriorly, terminating in one or two prolongations or cerci, while anteriorly there is a proboscis armed with strong setæ which may be invaginated within the anterior portion of the body, and serves as an organ of locomotion as well as for the prehension of food. The outer surface is covered by a layer of chitin which is divided into distinct metameric rings, the number of which, eleven, is constant for all known species, and which are provided in some species with definitely-arranged setæ. No cilia are present. Beneath the chitinous rings lies the ectoderm, which shows indications of metamerism also, being thickened beneath the interval between two successive rings; it consists of a granular layer of protoplasm in which scattered nuclei occur. Beneath the ectoderm lies a somewhat incomplete layer of longitudinal muscles, which become specialized anteriorly into separate bundles for the retraction of the proboscis; in each metamere two dorso-ventral muscle-bundles, one on each side of the middle line, are also found. A relatively spacious body-cavity in which various organs lie occurs, but no lining peritoneal epithelium or mesenteries have been observed.

The digestive tract begins with the mouth, which lies at the bottom of the invaginated proboscis and opens by the intervention of a short tube into a muscular pharynx into the anterior portion of which, four glands, either salivary or poisonous in function, pour their secretion. The pharynx communicates posteriorly with a sac-like stomach, upon which follows a short straight intestine opening to the exterior at the posterior end of the body between the terminal cerci.

Two elongated pear-shaped bodies lying in the cœlom in about the middle region of the body have been described as excretory organs. They are closed at the free end, their cavity is ciliated, and they open to the exterior on the dorsal surface near the margin of the body. The reproductive organs are cylindrical sacs which are provided with ducts opening to the exterior on the terminal segment; all the species whose reproductive organs have been studied are bisexual.

Four cellular masses lying above the pharynx seem to represent the nervous system, though no nerves passing from them have been discovered; nor do any special sense-organs exist.

The affinities of these forms is highly problematical, especially since nothing is known of their development. The metamerism indicated by the chitinous rings, the thickenings of the ectoderm, and the dorso-ventral muscles suggest an affinity with the Annelids, while, on the other hand, in the chitinous covering, and the occurrence of a longitudinal musculature only, similarities to the Nematodes may be found. The excretory organs may perhaps be compared with the larval nephridia of the Annelids, and the existence of but a single pair of them, together with the absence of any metameric arrangement of nerve-ganglia, favors the idea that the

Echinodera are not to be considered as being truly metameric, indications of metamerism which are found being altogether secondary and without phylogenetic significance. Until, however, something has been ascertained regarding their embryological history nothing can be positively stated as to their affinities. It is worthy of notice, however, that in some particulars they resemble the Gastrotricha, and it is not improbable that their nearest allies are to be found in that order, which on its part is related to the Rotifera (see p. 189).

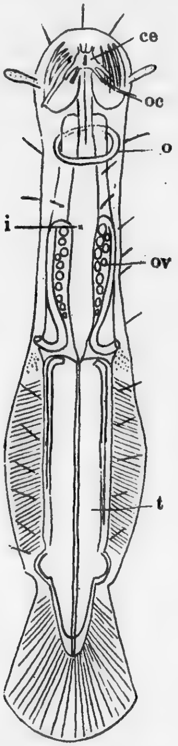

Fig. 92.—*Spadella cephaloptera* (after Hertwig).

ce = cerebral ganglion.
i = intestine.
o = olfactory organ.
oc = eye.
ov = ovary.
t = testis.

Class **Chætognatha.**

The Chætognatha constitute a small group of forms separable into two genera, *Sagitta* and *Spadella.* All the members of the group are marine, and are elongated in form, the sides of the body being furnished with one or two pairs of lateral expansions or fins, to which is added a caudal fin. The anterior portion of the body is somewhat enlarged so as to form a head, and on either side of the mouth are a number of strong chitinous bristles movable by means of special muscles and serving the purpose of jaws.

The ectoderm consists of several layers of flattened cells giving rise in the head region by secretion to chitinous plates which serve for the attachment of the muscles which move the jaw-bristles. Both the lateral and the caudal fins are ectodermal expansions consisting of a homogeneous lamella covered by one or two layers of ectodermal cells. They possess no muscle-fibres and are passive in locomotion, which is performed by the contraction of the longitudinal muscles producing rapid lateral movements of the posterior part of the body. The genus *Sagitta* possesses two lateral fins, while in *Spadella* (Fig. 92) but one large one is present. Below the ectoderm lies a well-defined basement-membrane, and below this are the muscles of the body-wall, which are, as a rule, longitudinal in their direction, and are interrupted, as in the Nematodes, along four longitudinal lines, one dorsal, one ventral, and two lateral. In one species of *Spadella* there is on the inner side of the longitudinal muscles a thin layer of transverse muscles, but usually only longitudinal fibres are present, except in the head, when there are a number of special muscle-bundles for the movement of the jaw-bristles.

Within the musculature of the body-wall is the spacious cœlom, lined throughout by a delicate layer of cells constituting the peritoneum, and divided into three chambers by transverse partitions, one of which lies just behind the head, while the other is towards the hind end of the body. The peritoneal epithelium lines the surfaces of these *dissepiments*, and in the trunk and tail regions is reflected in the mid-dorsal and ventral lines towards the centre of the body, forming a *mesentery*, surrounding the intestine and dividing the cœlom into lateral compartments.

The mouth lies on the ventral surface of the head and opens into an œsophagus surrounded by a single layer of muscle-fibres having a dorso-ventral direction and passing above and below into the general musculature of the head. After being narrowed in passing through the anterior dissepiment the digestive tube again expands (Fig. 92, *i*), and is supported throughout the trunk region by the mesentery. In this region it is a simple straight tube, unprovided with muscle-fibres, and terminates in an anal opening situated ventrally at the junction of the trunk and tail regions, not being continued into the latter.

Neither an excretory nor a blood vascular system is present. The nervous system lies for the most part imbedded in the ectoderm, and consists of two principal ganglionic masses, of which one, the cerebral or supraœsophageal ganglion (*ce*), lying in the head region, is situated in the ectoderm of the dorsal surface of the body and has a somewhat hexagonal outline, giving off five pairs of nerves, one pair passing backwards as commissures to unite with the ventral or subœsophageal ganglion, lying also in the ectoderm a little in front of the middle of the trunk region of the body. This ganglion gives off numerous nerves, among which are two principal nerve-cords passing backwards and giving off along their entire length finer nerves which branch and finally lose themselves in a fine ectodermal nerve-plexus throughout which ganglion-cells are scattered. In addition to these ectodermal portions three pairs of ganglia are found in the head region at the sides of the œsophagus, the largest ganglion on either side being united with the supraœsophageal ganglion by a commissure. From the supraœsophageal ganglia, behind the commissures to the ventral ganglion, a pair of nerves pass backwards to the two eyes (*oc*), which lie completely imbedded in the ectoderm of the dorsal surface of the head, each consisting of three biconvex lenses imbedded in a central pigment mass and surrounded on their outer surfaces by a retina composed of an outer layer of cubical cells, a middle layer of cylindrical cells with large nuclei, and an inner layer of rod-like structures arranged perpendicularly to the surface of the lenses. Behind the eyes lies a circular band of fine columnar ciliated cells (*o*), which is supplied by a pair of nerves arising from the supraœsophageal ganglion between the optic nerves. The function of this organ is doubtful, though it has been considered olfactory. Scattered somewhat regularly over the body are numerous round or oval eminences consisting of a number of central spherical cells arranged in two rows and bearing rod-like bristles. These are enclosed in a sheath of cylindrical cells and below come into contact or are continuous with terminal nerve-branches. These *sensory hillocks* are supposed to be tactile in function and resemble not a little the lateral sense-organs of certain Annelids (see p. 210).

The Chætognatha are without exception hermaphrodite. The ovaries (*ov*) are cylindrical bodies lying in the trunk region of the body, one on each side of the digestive tract, and upon the outer side of each is a tubular oviduct which ends blindly anteriorly and opens posteriorly at the sides of the body near the dissepiment between the trunk and tail regions of the body. There is no communication apparently between the cavity of the oviduct and the ovary or cœlom, and the manner in which the ova make their escape is yet unknown. Both ovaries and oviducts are enclosed within a fold of peritoneum (mesentery) extending from the sides of the body. The testes (*t*) are situated behind the posterior dissepiment, i.e., in the tail region of the body, and consist of a streak of cells on each side in the peritoneal covering of the body-wall. From these streaks masses of immature spermatozoa separate and float about in the cœlom of the tail segment, and when mature make their escape through canals, each of which communicates with the cœlom by means of a fine ciliated opening, and near its opening to the exterior at the side of the body is dilated into a seminal vesicle.

The embryological history of *Sagitta* throws no light upon the affinities of these forms. In structure they recall, especially in the arrangement of their musculature, the Nematodes, and especially the Gordiaceæ, but at the same time show many similarities to the lower marine Annelids, as for instance in the origin of the spermatozoa from the wall of the cœlom, and in the similarity of the vasa deferentia to nephridial canals. The occurrence of dissepiments also suggests affinities to the Annelids, but it does not seem that these structures indicate a segmentation of the body, since the arrangement of the nervous system points to the conclusion that the Chætognaths consist of a single segment. From the evidence at present open to us it would seem that the *Chætognatha* are more nearly related to the Annelids than to the Nematodes, but the relationship must be regarded as a rather remote one, and it seems hardly fitting to include *Sagitta* and its allies among the Annelida.

CLASS **ROTIFERA.**

The Rotifers or "Wheel-animalcules" are microscopic Metazoa which are widely distributed both in salt and fresh water. They are unsegmented forms with a well-developed cœlom, and are somewhat oval in form as a rule, the anterior end of the body being surrounded by one or two bands of cilia whose rapid movement produces the appearance of a wheel, and has suggested the popular name for the group. The posterior end of the body is frequently prolonged into a usually extensible so-called foot, which in some cases (*Lacinularia*) is furnished with adhesive glands, and is used as a point of fixation, though the majority of forms swim about freely or attach themselves only temporarily, the foot having in such cases the form of a sucker (*Philodina*), or terminating in two movable lamellæ, *Brachionus* (Fig. 93), or else being entirely wanting (*Asplanchna*).

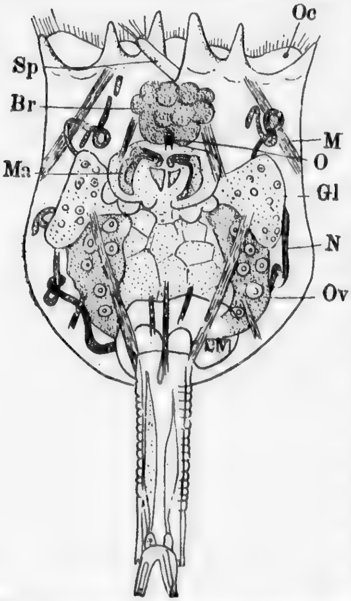

FIG. 93.—*Brachionus urceolaris* (after ECKSTEIN).

Br = nerve-ganglion.
cv = contractile vesicle.
Gl = digestive gland.
M = muscle.
Ma = mastax.
N = nephridial canal.
O = eye.
Oc = ocellus.
Ov = ovary.
Sp = calcar.

The body, with the exception of the anterior portion or *trochal disk*, which bears the bands of cilia, is enclosed in a chitinous cuticle, occasionally comparatively thick and firm, forming a case, the *lorica*, into which the softer parts may be withdrawn, and frequently presenting a delicate sculpturing or prolongations into spines. A few forms (*Floscularia*) secrete a gelatinous case within which they live, foreign particles being sometimes added to the secretion; a species of *Melicerta*, for instance, building a case for itself of pellets manufactured from foreign bodies and arranged in oblique or spiral rows and cemented together by the gelatinous secretion.

The *trochal disk* which occupies the anterior end of the body is but rarely circular in outline; more usually it is lobed at its margins and may even be separated into two parts. The margin of the disk is surrounded by one or two bands of cilia which follow the lobations, when two bands are present one being entirely præoral and the other postoral in its position, so that the mouth lies between the two on the ventral side of the disk. Various differences of arrangement of the bands are found in different species, one of them, the præoral, being some times discontinuous, as in *Brachionus*, or reduced to a few isolated patches, as in *Asplanchna*.

It is a question whether the forms with a double band of cilia or those in which it is single represent the more primitive arrangement. It may be supposed that originally there was but a single band which later became double, but it seems more probable that the double condition is the more primitive, from the fact of its frequent occurrence and also since, when a single band is present, it seems to represent in some cases the præoral band and in others (*Floscularia*) the postoral one. Such a condition of affairs can be most plausibly explained on the assumption that originally two bands were present, and that in some forms the præoral one gradually gained pre-eminence in its development, the postoral one disappearing *pari passu*, while in the Flosculariidæ the reverse was the case.

Beneath the cuticle lies the ectoderm, consisting of a layer of cells whose outlines cannot be distinguished, and within this comes the musculature of the body, which does not, however, form a more or less continuous layer beneath the skin, but consists of aggregations of muscle-fibres into bundles which traverse the body-cavity in various directions, some running longitudinally and forming retractors of the foot and of the trochal disk, while others have a circular direction. The cœlom, in which the muscle-bundles and the various organs lie, is not lined by a special peritoneal layer of cells, but may be traversed by a greater or less number of delicate fibrils arising from amœboid cells and representing undifferentiated mesoderm.

The mouth lies near the ventral border of the trochal disk, the ciliated bands serving to produce currents which converge toward the mouth-opening, and so carry to it food-particles, which are then carried through the ciliated œsophagus to the pharynx, whose walls contain a somewhat complicated comminuting apparatus, the *mastax* (Fig. 93, *ma*), consisting of two calcareous bodies, the *mallei*, of varying shape, and sometimes also of a median body, the *incus*. By the action of muscles attached to the mallei, these parts of the apparatus can be brought into contact with each other, and with the incus when this is present, the food-particles being thus comminuted. From the pharynx the food passes through a shorter or longer tube lined with chitin, which is to be regarded as a continuation of the pharynx, to the stomach, usually a globular cavity, whose wall is formed by a layer of ciliated cells containing fat-globules and various other particles, probably absorbed food-particles, these cells being covered externally by a layer of connective tissue. Into the stomach there opens from either side the duct of a gland (*gl*), whose secretion is probably digestive in function and which may be termed a *digestive gland* from its resemblance to similarly located glands in other invertebrates. The stomach opens below into the shorter or longer intestine, whose walls are lined by ciliated cells; and this in turn communicates with the terminal cloaca, which receives in some cases the terminations of the excretory tubules and may be contractile. The cloaca opens to the exterior, usually on the dorsal surface, near the base of the foot, though in some forms which live within a case the intestine bends forward upon itself, so that the cloacal opening lies further forward.

The nervous system consists of a relatively large ganglionic mass (*Br*) lying on the dorsal side of the œsophagus, from which nerves pass anteriorly to the trochal disk, and posteriorly to supply a dorsal sensory papilla, the *calcar* (*Sp*). In addition to this, two pairs of posterior nerves have been described, one of which passes to a sense-organ situated on each side of the body in its posterior third, while the other pair runs backwards on each side of the middle line to near the posterior end of the body, giving off branches to the musculature as it goes. Among the sense-organs eyes (*O*) are very generally present, varying in number from one to several, and situated in the region of the supraœsophageal ganglion, with which they are connected. They consist of patches of red, brown, or black pigment with which sensory or retinal cells are associated, and which are in some cases covered by a refracting lens formed as a special cuticular thickening. Other sense-organs to which a tactile function has been ascribed consist in their simplest form of one or several cells bearing stiff cilia. A pair of such organs is usually present, one on each side immediately above the ganglion of the lateral nerves, and anteriorly in the mid-dorsal line just behind the trochal disk a third occurs, the *calcar* (*Sp*), which frequently is situated upon the extremity of a tubular extensible process of the body-wall, supplied with muscles for its retraction, and to which nerve-fibres pass from the supraœsophageal ganglion. In a few forms, such as *Melicerta*, the calcar is double.

No blood vascular system exists, but a well-developed excretory apparatus (*N*), resembling that of the Turbellaria, is present. It consists of two longitudinal tubes, one on each side of the body, from which arise a varying number of finer lateral branches, each of which terminates in a funnel closed by a flame-cell, as in the Turbellaria. Anteriorly the two tubes may be united by a transverse connecting tube, and posteriorly they may unite together to form a contractile bladder which opens into the cloaca, or in some cases may open directly to the exterior.

The female reproductive apparatus consists of a relatively large ovary (*Ov*) which in some cases at least consists of a vitellarium portion and an ovary proper, the whole being surrounded by a thin membrane a backward prolongation of which forms an oviduct opening into the cloaca.

The preceding description of the structure of a Rotifer is that of such a form as is most frequently met with. It was for a long time believed that these were hermaphrodite, but no trace of a testis could be found. It was later found, however, that they were all females, and the males of several species have been discovered, differing decidedly in size and structure from the females, and besides being usually rather rare in their occurrence. They are considerably smaller than the female, and possess like it eyes, nerve-ganglion, muscles, and excretory system; but the ciliated band of the trochal disk is single, and the digestive tract, with the exception of the cloaca, is reduced to a solid band of tissue. The single testis occupies the greater portion of the body-cavity, and the short vas deferens opens into the cloaca, passing through an evertible intromittent organ. This marked difference of form of the male and female individuals of the same species constitutes a phenomenon known as *sexual dimorphism*. An explanation of the usual numerical preponderance of the females over the males is to be found in the fact that under favorable conditions the females produce ova capable of developing parthenogenetically, and giving rise in all cases to females. A series of generations reproducing by these so-called "summer ova" may thus succeed each other without the intervention of a male. Under certain conditions, however, certain females produce "summer ova" of a smaller size than usual, which, developing parthenogenetically, give rise to the males. In addition to these two forms of "summer ova," some species produce a third kind of egg, the so-called "winter ovum," which differs from the summer ova in containing more yolk and in being enclosed within a stout resistant shell. It seems probable that these ova develop only after fertilization.

There are two Rotifers which deserve a special description on account of their having served as a basis for phylogenetic speculation. One of these, *Trochosphæra* (Fig. 94), is spherical in shape ; a band of cilia runs round the equator of the sphere, not encircling it completely, however, but leaving an unciliated region on the dorsal surface. Anteriorly this band passes above the mouth-opening, which is bounded below by a very small post-oral band and opens into a pharynx provided with a mastax (*Ma*), from which the stomach, with digestive glands, passes towards the centre of the body and there bends at right angles to open through the intestine into a cloaca (*Cl*) which receives the excretory tubules (*Ex*) and the oviducts and opens to the exterior at the lower pole of the sphere (*A*). The brain (*N*) lies above the pharynx and sends nerves to the two eyes situated, one on each side, below the equatorial band of cilia, and also to a small sensory papilla (*So*), probably the calcar, lying on the dorsal surface, this nerve (*n*) encircling the anterior half of the sphere, and running in a plane at right angles to that in which the ciliated band lies.

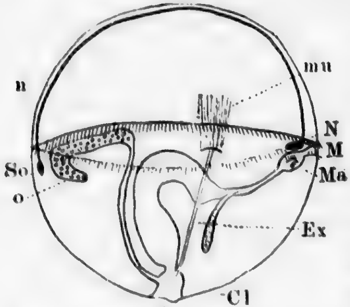

FIG. 94.—*Trochosphæra æquatorialis* (after SEMPER).

A = anus.
Cl = cloaca.
Ex = excretory tube.
M = mouth.
Ma = mastax.
mu = muscle.
N = nerve-ganglion.
n = nerve.
o = ovary.
So = sense-organ.

The other form belongs to the genus *Hexarthra* and differs from other Rotifers principally in the occurrence of six hollow processes of the body, arising from the ventral surface and arranged in pairs diminishing in size from before backwards. Each is terminated by a bunch of stiff bristles or setæ, and all are supplied with muscles whereby they can be rapidly swept backwards in the manner of a paddle and so serve as locomotor organs, producing a quick jerky movement quite different from the steady progression caused by the cilia of the trochal disk. In another nearly-related form, *Pedalion*, six processes are also present, but are arranged somewhat differently from those of *Hexarthra*, the largest one arising from the ventral and another from the dorsal surface, while the other four are lateral in position, two occurring on each side.

The Affinities of the Rotifera.—Several views have been advanced as to the affinities of the Rotifers, especially as regards their relationships to higher forms; these opinions will not, however, be fully considered here, but merely indicated, attention being directed first to the relationships in which the Rotifers stand to organisms lower in the scale. In this connection the excretory system becomes of no little importance on account of its resemblance to that of the Turbellaria, a resemblance which is further emphasized by the nervous system,—consisting of the simple brain, from which posteriorly-directed nerve-cords arise,—by the combined ovary and vitellarium, and by the absence of a blood vascular system. Here, however, the resemblance ceases, and the presence of an anal opening to the digestive tube marks the Rotifers as standing on a higher level than the Turbellaria. It seems probable, however, that the similarities do indicate the ancestry, and that the Rotifera have been derived from the Turbellarian type.

Another possibility which has been suggested is to the effect that they are derived from the form represented by the Trochophore larva of the Annelida (see p. 213). The principal argument for this view is found in the arrangement of the trochal cilia, which, in the occurrence in many cases of both præoral and postoral bands, certainly resembles not a little that of the Trochophore larva. It must be remembered, however, that the similarity in the arrangement of the cilia is not quite perfect, and that it may be without phylogenetic significance, having been acquired independently in the Rotifers and in the Trochophore larva; and furthermore it is noticeable that in one important character at least a marked difference is found, the nervous ganglion lying in the Rotifers behind instead of before the præoral band of cilia. The most that can be said at present is that the Rotifers show closer structural affinities to the Turbellaria than to any other group, and that it is probable that they represent the culmination of a line of development originating in that group, and furthermore that it is possible that they represent the ancestral annelid form indicated by the Trochophore larva.

Order Gastrotricha.

The Gastrotricha are minute forms, few exceeding 0.2 mm. in length, which occur in fresh water and have an elongated form flattened somewhat on the ventral surface, tapering posteriorly to end usually in one or two cercal processes, and anteriorly show a dilatation succeeded by a more or less well-marked narrow region, the two giving rise to a head and neck. The body is covered upon the outside by a cuticle, which may be smooth as in the genus *Ichthydium*, or take the form of overlapping scales as in *Chætonotus* (Fig. 95), sometimes bearing spine-like prolongations. Along the ventral surface two bands of cilia run from the posterior part of the head region almost to the hind end of the body, and in addition to these patches of cilia are found upon the ventral surface and on the sides of the head, some of which are undoubtedly sensory in function. Beneath the cuticular covering lies the ectoderm in the form of a layer of protoplasm in which no cell outlines can be perceived, but which contains numerous scattered nuclei. A pair of longitudinal muscle-bands lie beneath the ectoderm on the dorsal surface, and other bands traverse the cœlom in an antero-posterior direction. Transverse and circular muscles are, however, absent. A distinct cœlom is present, the greater portion of which is occupied, however, by the internal organs; it is not lined with a peritoneal epithelium, nor are any mesenteries present.

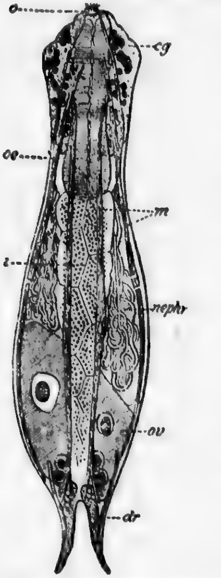

FIG. 95.—*Chætonotus maximus* (after ZELINKA).

cg = nerve-ganglion.
dr = glands.
i = intestine.
m = longitudinal muscles.
nephr = nephridia.
œ = œsophagus.
ov = ovary.

The mouth is situated at the anterior extremity of the body and opens into a muscular œsophagus (*œ*), which opens in turn into the cylindrical stomach (*i*). To this succeeds a short intestine opening to the exterior at the posterior extremity of the body.

No blood vascular system is present, but the excretory system consists of a single pair of much-convoluted tubes (*nephr*) which terminate at one end in a closed ciliated "funnel," while at the other they open on the ventral side of the body to the exterior. The reproductive system (*ov*) consists of two groups of germ-cells lying in the posterior part of the body, one on each side of the digestive tract, but no oviduct has been definitely made out to exist. With regard to the testes some uncertainty exists, an oval body lying in the same region of the body as the ovaries, but beneath the intestine, having been described as such an organ, though the identification is open to question. If, however, the body in question be the testes, the animals are hermaphrodite. As in the case of the female organ no ducts have been observed leading from the testes, and nothing is known as to the method by which the sexual products are extruded.

The nervous system (*n*) consists of a large ganglionic mass which lies above the œsophagus in the head region, and from the posterior border of which two processes, one on each side of the middle line, are directed posteriorly and dorsally, perhaps representing the origin of a pair of nerves, while the postero-external angles of the ganglionic mass are continued backwards to near the posterior extremity of the body to form the lateral nerves. Certain of the elongated cilia found on the head no doubt function as sense-organs, coming into intimate connection at their bases with the cells of the supra-œsophageal ganglion; in addition to these sense-organs eyes have also been described as occurring in some species, either in the form of simple patches of pigment lying in the integument above the brain, or else of such patches provided with lens-like structures.

The affinities of the *Gastrotricha* seem almost certainly to be with the Rotifera, many of the structural features being exceedingly similar in the two groups. The principal differences are to be found in the arrangement of the cilia and in the structure of the nephridia. With regard to the former it seems not improbable that in the arrangement seen in the *Gastrotricha* a relic of a more primitive uniform ciliation is presented, and that in this particular as well as in the greater simplicity of the digestive tract, and in the general form of the body and life-habits, the *Gastrotricha* approach more nearly an ancestral Turbellarian form than do the Rotifera. The nephridia depart much more widely, however, from the Turbellarian condition than do those of the Rotifera—a fact which argues against the more primitive character of the *Gastrotricha*, as does likewise the absence of ducts for the reproductive organs. Whether, therefore, the *Gastrotricha* are to be considered as representing the ancestral form from which both they and the Rotifera have descended more nearly than the latter group, or whether they are modifications of the Rotifer type of structure and have had for their ancestors forms which were Rotifer-like in structure, it is difficult to say; though the balance of evidence seems to tip in favor of the former view.

Attention should be called, however, to a possible affiliation of the *Gastrotricha* with the Echinodera. If, as has been suggested (p. 186), the segmentation of the latter has no phylogenetic significance, it is not difficult to trace similarities of structure in the two groups, the principal differences being connected with external parts. It is by no means improbable that the Gastrotricha, Rotifera, and Echinodera form a series, each of the groups being of equivalent rank, and related to each other somewhat as are the Turbellaria, Trematoda, and Cestoda.

Genus **Dinophilus.**

The genus *Dinophilus* includes some small marine organisms all of which are referable to a small number of species. The body (Fig. 96) is cylindrical and consists of a head segment followed by from 5–7 trunk segments (the number varying according to the species), each of which bears a ring of cilia, interrupted ventrally by a uniform ciliation which covers the entire ventral surface. The head is likewise provided with a ring of cilia which is usually double, one of the constituent bands passing in front of the mouth and the other behind it, the area intervening between these two bands being, in one species at least, occupied by smaller cilia. The musculature of the body-wall is but weakly developed, though both an external layer of circular fibres and an internal one of longitudinal fibres may be found, both layers being absent in one species in the dorsal region. The cœlom is traversed by a network of branching cells, there being no special peritoneal layer, and no musculature in the walls of the intestine.

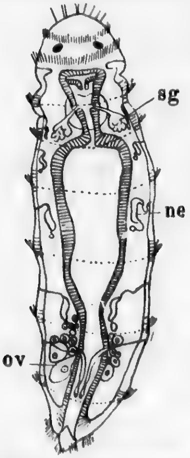

FIG. 96.—*Dinophilus gyrociliatus* (after MAYER).
ne = nephridium.
ov = ovary.
sg = salivary gland.

The mouth is situated on the ventral surface at the junction of the head and first trunk segments, and leads into a wide ciliated œsophagus, beneath which lies a muscular proboscis contained in a special sheath and protrusible through the mouth-opening. Behind the œsophagus is a *proventriculus*, a small thick-walled ciliated cavity, into which, at its junction with the œsophagus, a pair of salivary glands (*sg*) pour their secretion. Behind, the proventriculus communicates with a cylindrical stomach, upon which follows the short straight intestine, terminating in the anus at the posterior end of the body.

There is no blood vascular system. An excretory system is present, consisting in *D. gyrociliatus* and *D. tæniatus* of five pairs of nephridia (*ne*) which open externally on the sides of the body and terminate in the cœlom-spaces in a funnel containing a flame-like bunch of cilia. Whether a direct communication between the lumen of the nephridial tubes and the cœlom exists in all cases has not been definitely ascertained, but a similarity of structure to the Platyhelminth type of nephridium is shown by the flame-like bunch of cilia and by each nephridium being composed of a series of perforated cells. The reproductive organs are separated in different individuals; and in one species, *D. gyrociliatus*, a marked sexual dimorphism similar to that occurring in the Rotifera exists, the male being much smaller than the female and possessing only the ciliated ring of the head and the ventral ciliation; and furthermore the digestive tract and the principal sense-organs are entirely wanting. The reproductive elements (*ov*) are shed into the cœlom-spaces and find their way to the exterior in some species at least by means of the most posterior pair of nephridia, which in the male of *D. tæniatus* are transformed into seminal vesicles and are connected with an intromittent organ situated in the posterior segment.

The nervous system consists of a brain or supracœsophageal ganglionic mass which occupies the greater portion of the head segment and from which two nerve-cords pass backwards in the lateral region of the body, and in *D. tæniatus* possess ganglionic enlargements equal in number to the pairs of nephridia and the trunk segments and are connected by transverse commissures. In other species, however, these structures have not been observed. Eyes occur imbedded in the substance of the supracœsophageal ganglion, and tactile hairs occur at various regions of the body.

Affinities of Dinophilus.—The descriptions given of the various known species of *Dinophilus* indicate a considerable variation in the structure of certain parts, more especially of the nervous system, which in *D. tæniatus* partakes of the metamerism shown by the nephridia and the bands of cilia, while in other forms it is apparently non-metameric. This would indicate either that the metamerism has been acquired within the limits of the genus, or else that those forms lacking it are degraded in this respect and have descended from metameric ancestors. There is little justification to be found, however, for the calling in of degradation to explain obscure relationships unless there is sufficient collateral evidence to support such an appeal ; in the present case this seems to be absent, and the marked similarity of the non-metameric nervous system to that of the Turbellaria suggests an origin from these forms and favors the first hypothesis as to the origin of the metamerism. The nephridia also and the character of the cœlom strengthen the probability of a Turbellarian ancestry.

A close relationship to the Rotifera has also been suggested and is not debarred by the supposition of a descent from Turbellarian forms ; but it seems doubtful if such a relationship can be other than a very distant one. The position of the supracœsophageal ganglion relatively to the cephalic cilia or *prototroch*, and the paired arrangement of the nephridia as well as the occurrence of circular fibres in the subepidermal musculature, stand in opposition to the view, and the most that can be said is that both *Dinophilus* and the Rotifera are to be referred back to closely-similar ancestors.

The affinities of *Dinophilus* and the Rotifers to the Annelida will be discussed in connection with the latter group (p. 217).

SUBKINGDOM METAZOA.

Order *Echinodera.*—Body cylindrical, with 11 rings ; no cilia ; with proboscis ; minute forms ; marine. *Echinoderes.*

Class CHÆTOGNATHA.—Marine ; body divided into three segments ; with lateral and tail fins ; mouth with chitinous jaws composed of series of strong bristles. *Sagitta*, *Spadella.*

Class ROTIFERA.—Anterior end provided with a retractile crown of cilia ; minute forms both aquatic and marine. *Floscularia*, *Melicerta*, *Lacinularia*, *Philodina*, *Brachionus*, *Asplanchna*, *Trochosphæra*, *Pedalion*, *Hexarthra.*

Order *Gastrotricha.*—Minute forms both marine and aquatic ; ventral surface of body ciliated ; no anterior crown of cilia. *Ichthydium*, *Chætonotus.*

Genus *Dinophilus.*—Small marine forms ; body with 5–7 segments, each with a ring of cilia.

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CHAPTER X.

TYPE ANNELIDA

The type *Annelida* includes a series of forms among which metamerism reaches a high grade of development. In what may be considered a typical Annelid (Fig. 97) a number of segments or metameres succeed one another from the head to the tail, each one resembling its predecessor and its successor in all its parts; the nephridia, reproductive organs, nerve-ganglia (*n*), and appendages, when present, are repeated in each successive segment, and each metamere is marked off from its fellows, externally by a groove surrounding the body and internally by a partition or dissepiment extending transversely across the cœlom from the body-wall to the digestive tube. This latter structure and the blood vascular tubes cannot well from the nature of things be divided metamerically, but are continuous from one end of the body to the other, showing, however, in the metameric pouches and intermetameric constrictions of the digestive tract, and in the metamerically arranged lateral vessels of the blood vascular system which encircle the digestive tube, indications of the division which has affected the other organs.

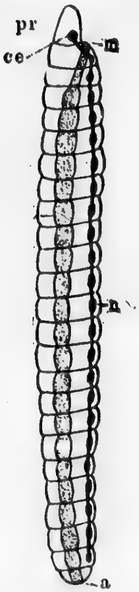


Fig. 97.—Diagram of General Plan of an Annelid.

a = anus.
ce = cerebral ganglion.
m = mouth.
n = ventral nerve-cord.
pr = prostomium.

Two segments, however, the head (*pr*) and the tail, usually present differences from the rest in their structure; the head or anterior metamere bears sense-organs when these are developed, is destitute of nephridia in the adult, and contains primarily the supracœsophageal ganglion of the nervous system (Fig. 97, *ce*), the ganglia of the trunk metameres (*n*) lying ventrally to the digestive tube; while the tail segment bears the anal opening and usually presents other characteristics which distinguish it from the preceding segments. It is rare, however, leaving aside this antero-posterior differentiation, that a perfect metameric condition is found in any Annelid. Secondary changes may interfere with the similarity of all the metameres; a suppression of parts usually present in some of the segments may occur, as, for instance, where the reproductive organs are confined to one or two metameres, or again there may occur a differentiation of the anterior appendages for a special function whereby a marked dissimilarity between the anterior and posterior metameres is produced. Finally, owing to peculiar habits of life, the metamerism may be almost or completely lost, being indicated only, perhaps, by one set of organs, such as the nerve-ganglia, or else only evident in the larval stages. Parasitism or a fixed or tubicolous habit of life are among the principal causes of this degeneration, examples of which will be seen later.

In consequence of this degeneration some Annelids present a metamerism of a lower grade than that found in such forms as the Nemerteans. Other peculiarities of structure occur, however, which serve, together with the indications of metamerism, to mark out the Annelid type. One of these peculiarities is the occurrence in nearly all forms of a series of nerve-ganglia along the ventral nerve-cords; this feature is of course a part of the metamerism, but it is not usually marked in the metamerism of the nervous system seen in lower forms. In these scattered ganglion-cells occur all along the nerve-cords, which extend backwards from the brain, while in the Annelids these scattered cells are associated together to form metameric ganglia. Another peculiarity is found in the structure of the nephridia. These are no longer in all cases rows of perforated cells closed at the inner end by a flame-cell, but may consist of more or less convoluted tubes lined by ciliated epithelium and open as a rule into the cœlom by a wide funnel-like extremity. Provisional kidneys of the Turbellarian type occur in the larvæ of many Annelids, but the nephridia of the adult are, as a rule, of the character just indicated and depart widely from the Turbellarian character. In the third place the reproductive organs are developed in the peritoneal lining of the cœlom and are not usually (except in the Hirudinea) provided with special ducts. When mature the ova or spermatozoa are simply shed into the cœlomic cavity and make their way to the exterior through the ordinary nephridia, or through nephridia specially modified for the purpose. Finally it may be mentioned that a blood vascular system is usually present.

I. CLASS **Chætopoda.**

The Chætopoda are Annelids in which the external segmentation of the body corresponds with the internal segmentation of the organs, and which bear along the sides of the body two rows of pouches, the *seta-sacs*, the cells lining which secrete chitinous spicules or *setæ* of various shapes, which serve for the purpose of locomotion or in some cases constitute a defensive armament.

The class is conveniently divisible into two subclasses.

Subclass I. **POLYCHÆTA.**

The forms included in this subclass are exclusively marine, and are characterized by the presence on the sides of a greater or less number of the metameres of a pair of hollow processes of the body-wall upon which the seta-sacs occur and which are known as *parapodia*. In a few forms (*Serpula*) the parapodia, and indeed the setæ as well (*Polygordius*), may be absent, and in others, such as *Clymenella*, they may be very much reduced in size, but as a rule they possess a high degree of development. In its typical form a parapodium (Fig. 98) consists of a dorsal and a ventral lobe each of which bears seta-sacs and setæ (*s*). Towards the base of each lobe there may frequently be found a slender hollow process, the dorsal and ventral *cirrus* (*dc* and *vc*), and plate-like or more or less dendritic appendages, the *branchiæ* (*br*), either modifications of the cirri or branches arising from them, and respiratory in function, also occur. Muscles pass from the body-wall to the parapodia, which thus become important organs of locomotion and in some of the actively swimming species assume a more or less flattened plate-like form.

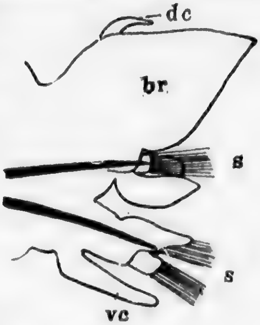


FIG. 98.—PARAPODIUM OF *Nereis virens*.

br = branchia.
dc = dorsal cirrus.
s = setæ.
vc = ventral cirrus.

The head segment is generally well differentiated from those which succeed it, being destitute of parapodia and setæ, and as a rule carrying a number of appendages sensory in function, and being likewise usually provided with eyes. The cephalic appendages may be short and rather stout, forming what are termed *palpi* (Fig. 100, *p*), or somewhat longer and more slender, forming the *cirri* (*c*), or even still more slender, being then known as tentacles (*t*).

The body is enclosed in a chitinous covering secreted by the subjacent ectoderm, here known as the *hypodermis* (Fig. 99, *hy*). The musculature of the body-wall which lies below the hypodermis is separated from this by a basement-membrane and consists of an external layer of circular fibres (*cm*) and a subjacent layer of longitudinal fibres (*lm*) which is, as a rule, interrupted in the mid-dorsal and ventral lines and also in the region of the two lobes of the parapodia so as to form four bundles. Special muscles extend from the body-wall to the base of the seta-sacs, and furthermore a pair of muscle-bands cross the cavity of each metamere, in typical cases passing from the lateral regions of the dorsal surface downwards and inwards to be inserted into the ventral body-wall on each side of the median line. The inner surface of the longitudinal muscle-layers is lined with a layer of *peritoneal cells* which completely enclose the cœlom (*co*) of each metamere, being reflected upon the surfaces of the dissepiments which form the internal partitions between adjacent metameres. The separation of the cœlomic cavities of the metameres is, however, rarely perfect, openings occurring here and there in the dissepiments, and in some forms, such as *Capitella*, a number of the dissepiments may at the breeding season completely degenerate so that the cavities of the various metameres concerned become perfectly continuous. The cœlom of each metamere consists in reality of two sacs which are folded around the digestive tract, which they enclose, and come into contact with each other above and below the intestine, forming the dorsal and ventral *mesenteries* (Fig. 99, *dm* and *vm*). That wall of each sac which lines the musculature of the body-wall is termed the *somatic* layer of the peritoneum, while that surrounding the digestive tract is the *splanchnic layer*.

The blood vascular system consists of a dorsal vessel (Fig. 99, *db*) which runs along the mid-dorsal line of the digestive tract and which is frequently contractile in portions of its course, serving as a heart, and a ventral vessel (*vb*) lying below the digestive tract, and being connected with the dorsal vessel by lateral trunks, arranged metamerically. From these vessels branches are distributed to the various regions of the body. The blood is frequently colored, usually red, and contains colorless corpuscles, the coloring-matter being dissolved in the plasma in which the corpuscles float. The blood vascular system is completely closed throughout its entire course, never opening into sinuses without definite walls. In addition to the blood which circulates within this definite system of tubes the cœlom also contains a corpusculated fluid, frequently colored and approaching blood very closely in its characters. This *hæmolymph* contains corpuscles, usually amœboid in form, and may circulate through the body from one metamere to another through openings in the dissepiments. In a few forms, such as *Capitella*, it may fulfil the functions of the blood, a true blood vascular system being wanting, and in this case contains, in addition to the colorless amœboid corpuscles, others which are disk-shaped and pigmented. It seems probable, however, that the absence of a true blood vascular system is a purely secondary phenomenon, and accordingly does not indicate a primitive condition.

The mouth is situated on the ventral surface of the body, at the junction of the head metamere with the first trunk metamere, and leads in many forms into a strongly muscular, usually protrusible pharynx provided with chitinous teeth. Upon the pharynx follows the usually straight intestine which opens to the exterior at the posterior extremity of the body. In *Capitella* and the allied genera, as well as in certain members of the family Eunicidæ, an *accessory intestine* lies ventrally to the principal one, into which it opens either both anteriorly and posteriorly or else anteriorly alone. This accessory intestine is ciliated and seems never to contain food-matter; it has been considered to be respiratory in function and seems to be a special development of a ciliated groove which runs along the ventral surface of the intestine in certain other forms. Pouch-like outgrowths of the intestine are frequently present and may sometimes become essentially glandular in function. In *Hesione* and in certain species of *Syllis* pouches communicating with the anterior part of the

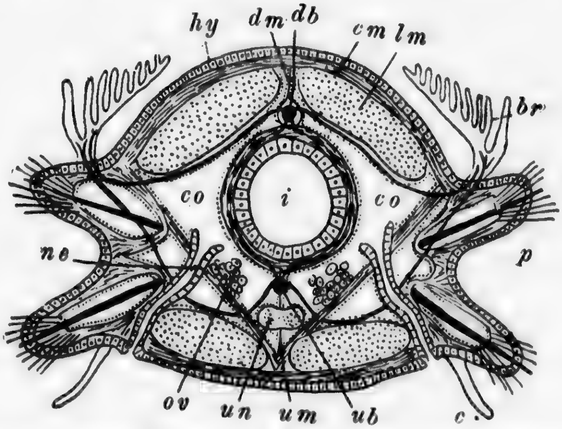


FIG. 99.—DIAGRAM OF TRANSVERSE SECTION OF ANNELID (combination of figures by LANG and EHLERS).

br = branchia.
c = cirrus.
cm = circular muscles.
co = cœlom.
db = dorsal blood-vessel.
dm = dorsal mesentery.
hy = hypodermis.
i = intestine.
lm = longitudinal muscles.
ne = nephridium.
ov = ovary.
p = parapodium.
ub = ventral blood-vessel.
um = ventral mesentery.
un = ventral nerve-cord.

digestive tract occur, which normally are filled with air and are richly supplied with blood-vessels; they may be respiratory in function, and have been compared to the swim-bladder of fishes.

The nervous system is well developed in all Polychæta, and consists of a *supraæsophageal* ganglionic mass situated in the head segment, frequently presenting a division into several lobes. From it various nerves arise passing to the anterior segment, and in addition a strong cord passes from it ventrally on either side of the œsophagus to unite with a ganglion lying below the œsophagus in the second metamere, forming the *circumœsophageal commissure*. To the *subœsophageal ganglion* of the second metamere there succeeds a pair of ganglia in each metamere, each pair being united with the preceding and succeeding pairs by two longitudinal cords of nerve-fibres, the *connectives*, the whole constituting the ventral nerve-chain, and furthermore the ganglia of each pair are united by a transverse commissure. The ventral nerve-chain has therefore a distinctly ladder-like arrangement, frequently somewhat obscured, however, by the approximation of the ganglia of each pair and a consequent shortening of the transverse commissures. From the various ganglia nerves arise which pass to the musculature of the metameres and to the hypodermis and its sense-organs. In the majority of forms the nervous system lies freely in the cœlom surrounded by a special sheath, but occasionally in various forms widely separated genetically from one another, such as *Polygordius* and the Opheliaceæ, it presents a primitive character in being completely imbedded in the hypodermis, recalling the condition in certain Nemerteans and in the Cnidaria. Special nerves arising from the supraœsophageal ganglion are supplied to the walls of the digestive tract, forming the so-called *stomatogastric* nerves.

Sense-organs of various kinds are of frequent occurrence at different portions of the body of the Polychæta. In addition to the cephalic and caudal cirri which are richly supplied with nerves and are presumably tactile in function, eyes are of very general occurrence. They are usually situated on the head, sometimes in connection with the hypodermis and sometimes imbedded in the dorsal surface of the brain. For the most part they consist of a cup of pigment-cells, in which numerous sensory cells are present—a lens being in some instances developed above each eye. Occasionally, however, as in the pelagic genus *Alciope*, the eyes reach a high grade of development. In some forms they are not confined to the region of the head, as for instance in the genus *Polyophthalmus*—so named from the fact that pairs of eyes are found on the sides of a number of the trunk metameres; in the majority of tubicolous Annelids eyes are found in considerable numbers upon the branchial lobes of the head segment, the genus *Vermilia* possessing somewhere in the neighborhood of 11,000 separate ocelli in this region. These eyes are simply differentiations of the ectoderm, and in many cases are still situated in the hypodermis; they consist of a number of cells which are prolonged at their inner ends into a nerve filament, while peripherally their protoplasm is converted into a refractive substance, each of these cells being separated from its neighbors by pigment deposited in its peripheral layers, as well as by a number of smaller pigment-cells. On account of this pigment-sheath it is presumable that each of these optic elements or *ommatidia* functions more or less independently of the rest, and the eyes are to be considered as compound, composed of a number of independent parts each of which is physiologically an eye.

Auditory organs or otocysts also occur in certain forms, but cannot be considered as typical of the Polychæta. In *Arenicola* they consist of two sacs lying in close proximity to the circumœsophageal commissures and connected with the exterior by a narrow canal, indicative ot their origin as invaginations of the hypodermis. The walls of the sack are formed by columnar cells terminating below in a plexus of nerve-fibrils and covered on the surface turned towards the cavity of the otocyst with a firm homogeneous cuticle, and not possessing any terminal hairs. In the cavity a varying number of spherical particles of carbonate of lime, the otoliths, are found. In some forms a number of such otocysts are present, as in *Aricia*, where four or five pairs have been found in adult individuals; but in the majority of species they do not seem to be developed.

Ciliated depressions which have been supposed to be olfactory have been described as occurring in the anterior region of the body in various species, reaching a high development in the Capitellidæ, where they form club-shaped sacks capable of being evaginated. In addition there are to be found scattered on the surface of the body minute *beaker-shaped* depressions, at the bottom of which are cells bearing long hairs and presumably sensory in function; and furthermore in a few forms, such as the Capitellidæ and *Polyophthalmus*, a series of sensory hillocks occur along the sides of the body—a pair in each metamere, forming the *sense-organs of the lateral line*. In the Capitellidæ these organs are in the anterior metameres contained in depressions, but more posteriorly they project slightly from the surface. The central part of each projection is retractile and is formed of a number of hair-cells, each of which is in connection at its inner end with a nerve-fibril. No little interest attaches to these organs, which forcibly recall, both in their structure and distribution, the lateral line organs of the lower Vertebrates.

The nephridia (Fig. 99, *ne*), in typical adult forms, occur as a single pair in each metamere except the two terminal ones. Each consists of a usually contorted or coiled tube lined with cells opening by a funnel-shaped mouth into the cœlom of the metamere, perforating the dissepiment between it and the next metamere in which the greater portion of it lies and in which it opens to the exterior by a small pore situated on the ventral surface of the body at the base of the parapodium. It is rare, however, that any such metameric regularity of arrangement occurs, and very frequently they become reduced to a small number, or even to two pairs; in the tubicolous forms a few pairs are frequently found in the anterior portion of the body much larger than any of the rest. In addition to their original excretory function they may also serve as outlets for the reproductive elements, and in some cases become specially modified for this purpose and lose their original function.

In *Capitella* only one pair, that of the eighth metamere, becomes converted into a genital duct; and it is interesting to note that in this same segment a true excretory nephridium is also present. Whether this indicates or not the occurrence originally of more than one pair of nephridia in each metamere remains to be seen, but it is interesting in connection with what occurs in the Oligochæta (see p. 223).

The reproductive organs consist of local thickenings of the peritoneal epithelium (Fig. 99, *ov*) in more or fewer of the segments. The ova or spermatozoa fall when ripe into the cœlomic cavity and pass to the exterior by the nephridia. With very few exceptions the Polychæta are bisexual.

The classification into smaller groups is to a certain extent artificial at present, and does not profess to have any phylogenetic significance. Three orders may be recognized.

1. Order **Archiannelida.**

This order includes a few forms which are supposed to present more primitive structural characteristics than the remaining Polychæts. They show as a rule but indistinct traces of an external segmentation, and are entirely devoid of either parapodia or setæ. Tentacles occur at the anterior extremity of the head metamere; but no other appendages, such as cirri or branchiæ, occur. The nervous system is imbedded in the hypodermis, and the nephridia are short tubes, a single pair occurring in nearly every segment. To this group belong the genera *Polygordius* and *Protodrilus.*

2. Order **Errantia.**

In this order are placed the free-swimming or creeping Polychæta, in which a considerable similarity of the various trunk metameres occurs. The parapodia are as a rule well developed, and occasionally are broad and plate-like in adaptation to a free-swimming existence. Branchiæ are usually found on the dorsal lobes of a considerable number of parapodia; the head is distinctly marked off from the trunk and may bear eyes; while the anterior portion of the digestive tract is converted into a protrusible pharynx, usually armed with chitinous teeth. To this order belong the genera *Nereis* (Fig. 100), usually found lurking beneath stones during the day-time, but becoming, in some species at least, free-swimming at night; *Lepidonotus*, characterized by the possession of elytra arranged in overlapping series on the dorsal surface; *Diopatra*, which forms tubes for itself by gluing together particles of foreign matter; and *Autolytus* and *Syllis*, which are peculiarly pelagic in habit, as is also *Alciope*, characterized by its large highly-organized eyes.

3. Order **Sedentaria**.

This order includes a number of forms which manufacture for themselves tubes of various substances—some being merely composed of particles of sand glued together by an adhesive secretion, while others consist of a chitinous substance, to which foreign bodies may be added, or even of carbonate of lime. Within these tubes the animals permanently reside, and in conformity with this mode of life numerous adaptations of structure are found. The head is usually provided with a number of long cirri and the branchiæ are for the most part confined to the head region. In some forms, such

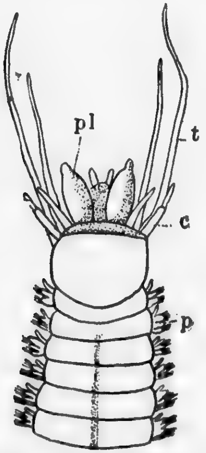


FIG. 100.—ANTERIOR END OF *Nereis virens*.
c = cirrus.
p = parapodium.
pl = palp.
t = tentacle.

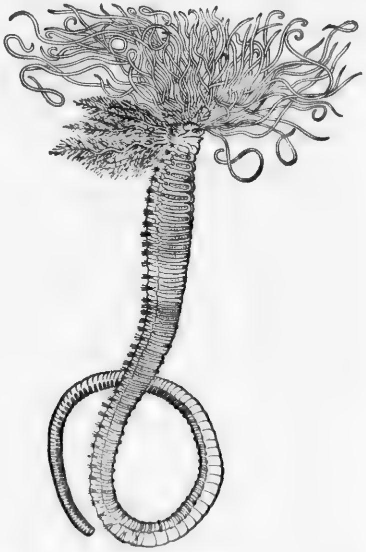


FIG. 101.—*Amphitrite ornata* (after VERRILL).

as *Serpula* and *Sabella,* plume-like branchiæ supported by an axial cartilage-like skeleton occur upon the sides of the head, and numerous eyes may be found in the hypodermis of these structures. Parapodia are as a rule but slightly developed, sometimes being entirely wanting though the setæ persist, those of the lower parapodial lobe being usually hook-like. The protrusible pharynx with chitinous teeth does not for the most part occur. *Amphitrite* (Fig. 101) lives in tubes in sand, while *Terebella* composes tubes by gluing together particles of sand. In *Sabella* the tubes are membranous in character, while *Serpula* manufactures more or less contorted tubes of carbonate of lime.

Development of the Polychæta. — An important feature in the development of the Polychæta is the occurrence of the *Trochophore* larva. A typical example of this larva is to be found in the development of *Polygordius*; it is a transparent organism, having the form of two low cones united by their bases (Fig. 102). Just below the junction of the two cones is the mouth (*M*), leading by a short *stomodæum* or œsophagus into a retort-shaped stomach, the intestine opening at the apex of the lower cone. Above the mouth, along the line where the two cones are united, lies a band of strong cilia arranged in two rows and forming an almost complete girdle for the body, being wanting, however, in the mid-dorsal region. This is the *prototroch* (*pro*) or præoral band of cilia, and parallel to it is a second weaker band which passes behind the mouth—the *paratroch* (*po*) or postoral band. The slight [illegible] between the two bands is lined by fine cilia, the adoral cilia, and in some Trochophores a band of fine cilia extends backwards along the ventral surface of the body towards the apex of the lower cone.

At the apex of the upper cone is a strong thickening of the ectoderm, the *apical plate* (*ap*), which is nervous in function and bears a number of strong cilia and may also have imbedded in it pigment-spots which function as light-percipient organs. From the apical thickening four nerve-cords (*n*) extend backwards, one being dorsal, the other ventral, and the remaining two, stronger than the others, lateral. A series of fine nerve-rings arranged concentrically about the apical thickening unite these cords at regular intervals, the lower ring being connected with the cells which bear the protrochal cilia and forming the *prototroch nerve.*

At the apex of the lower cone and ventral to the intestine lie two cells, or two masses of small cells, which constitute the mesoblasts and give rise to two longitudinal mesoblast bands (*mb*). A few scattered cells are also found between the ectoderm and the digestive tract, some of which elongate and become muscle-fibres (*m*), and which have been thrown off from the mesoblast bands. In some forms a band of muscle-fibres underlies the prototroch cells. In the neighborhood also of the mesoblast bands in the posterior cone there occurs on either side of the digestive tract a small, sometimes branched, tubular body, the head-kidney (*ne*). Each kidney consists of a row of perforated cells, terminating in a funnel-shaped structure closed at its mouth by a cell, the whole structure thus agreeing closely with the nephridia of the Platyhelminths.

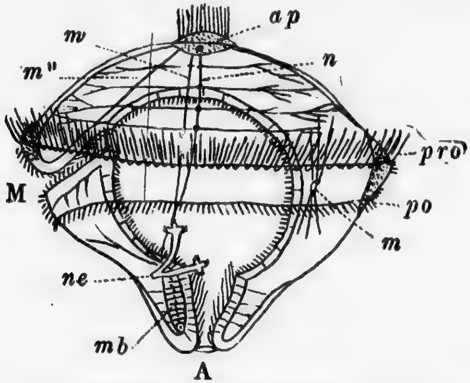


FIG. 102.—TROCHOPHORE OF POLYGORDIUS (after HATSCHEK).

A = anus.
ap = apical plate.
M = mouth.
m, m', m'' = muscles.
mb = mesoblast-band.
ne = nephridium.
pro = præoral band of cilia.
po = postoral band of cilia.

From such a larva the adult condition is derived by the gradual elongation of the posterior part of the body—an elongation with which the mesoblast bands keep pace, the mesoblasts retaining their position at the posterior extremity, and continually adding to the bands by the formation of new cells. The bands as growth proceeds break up into a number of masses, the mesoblastic somites, in the interior of which cavities appear, and adjacent pairs of masses growing dorsally and ventrally finally come into contact above and below the digestive tract, the dorsal and ventral mesenteries of the intestine being thus formed, and later a metamerization of the body-wall, corresponding with that of the mesoderm, also takes place. The anterior cone of the larva, which at first surpassed in size the posterior one, gradually becomes smaller, and the prototrochal cilia, and in some cases the cells also, are thrown off. The apical plate takes part in the formation of the supraœsophageal ganglion of the adult, and the lateral nerve-cords arising from it form the circumœsophageal commissure, becoming connected with thickenings of the ventral hypodermis arranged metamerically and representing the ventral chain of ganglia. The head-kidneys gradually disappear, being merely provisional larval structures, and new nephridia of the Annelid type develop from the mesoderm of the trunk-metameres.

Although the Trochophore larva occurs in the life-history of many of the Annelids, as well as in other groups as will be seen later, yet nevertheless it is not invariably present. In some forms a single band of large cilia runs around the middle of the body, which is elsewhere uniformly ciliated, while in others the cylindrical larva is surrounded by several bands of cilia succeeding one another at definite intervals. In certain species the larva is provided with very long setæ which are thrown off during larval life, and are interesting on account of similar setæ having been found in fossil forms, though absent in recent adult species.

It is also worthy of note that in some forms the Trochophore larva is succeeded by a well-marked stage in which, in addition to the head segment, three trunk segments are developed. It is possible that this may represent an ancestral form from which certain other groups have taken their origin.

In what may be considered exceptional cases a non-sexual reproduction by budding also occurs. In the genus *Protula* a zone of growth occurs in the sixteenth segment, and at this point later separation takes place, a new head developing for the posterior individual from the original seventeenth segment. In one species of *Syllis* the new individuals arise not only in a linear series but also as lateral buds, so that a branching colony is produced ramifying through the canal system of the Hyalosponge in which the form lives. The buds eventually separate as sexually mature male and female individuals which, since they differ from the parent form in possessing more highly developed eyes as well as a more perfect adaptation of the parapodia for swimming, probably leave the sponge and swim about freely in the ocean distributing their sexual elements. If this be the case, this species presents both colony formation and alternation of generations, the latter phenomenon being also manifested by other species of *Syllis* and by *Autolytus*, in which buds are produced linearly, differing from the parent in the structure of the parapodia and separating to lead a free existence as male and female individuals. A modification of this process is found in certain species of *Nereis*, in which at the time of sexual maturity the posterior segments of the body develop setæ more perfectly adapted for active locomotion by swimming than were those of the immature form; these sexually mature forms were at one time referred to a separate genus, *Heteronereis*.

The Phylogeny of the Polychæta.—The origin of the Polychæta has been within recent years the subject of considerable discussion. The discovery of the wide distribution of the Trochophore larva led to the supposition that it was an ancestral form, from which the Polychæta had been developed by a process of linear budding, each metamere of the Polychæt body being equivalent to the original Trochophore and the adult organism being a co-ordinated succession of Trochophore individuals. Other authors, however, who do not see in metamerism the result of a budding of the individual, but rather the multiplication of its subordinate parts, are inclined to refer the Annelids to a Nemertean-like ancestor and to consider the Trochophore larva a purely secondary adaptation. Between these two views it is difficult to decide, and it is possible that in their plain statement neither is quite correct, though each may contain certain elements of truth.

It seems exceedingly probable that a larval form which is met with in the life-history of the Annelids and Mollusca, as well as in a modified form in other groups, has some ancestral significance. It is difficult on any other hypothesis to explain its occurrence in widely different groups, since it seems hardly probable that it could have arisen independently in several instances. Convergent evolution could hardly be carried to such an extent as to produce in the Mollusca, quite independently of any genetic relationships, a larva resembling in all its structure that of an Annelid. If the Trochophore occurred only in the Annelids, it might be quite possible that it had made its appearance in the life-history of some primitive Annelid as a secondary modification of a more primitive larva, and had reappeared subsequently in the life-history of all forms descended from this Annelid ancestor, but this would not explain its occurrence also in the Mollusca, unless it be supposed that the members of this group have been derived from the primitive segmented Annelid, a view that has little to recommend it. The working of the biogenetic law (see p. 143) is interfered with in innumerable instances, and the distinguishing between examples of its action and secondary modifications is the most difficult task of the embryologist. The evidence at present available seems, however, to point, in the case of the Trochophore, to its being an example of the law, and to this extent the first of the two views stated above is probably correct.

But, on the other hand, this may not be the case with the second part of the theory. If the view as to the origin of metamerism which is advocated in this work be correct, then the Annelid cannot be regarded as having arisen directly by a process of reproduction by budding of the Trochophore. It is not a colony of Trochophore individuals, but a single elongated Trochophore whose organs have undergone repetition, producing a high grade of metamerism. To this extent the second of the views may be correct, but this does not necessarily imply that the Annelids are to be derived from a Nemertean-like form in which the metamerism is not quite so perfect. Metamerism, as here explained, is simply the following out into the higher individualities of the phenomenon of discontinuous growth or reproduction by division which characterizes the cell, and it is quite possible that there may be no more genetic connection between the metamerism of the Nemertean and that of the Annelid than there is between that of the Cestode and that of the Nemertean. It may have arisen quite independently in the two forms, and in fact when the details of metamerism are examined in the two groups considerable differences are to be seen.

The view here advocated in regard to the origin of the Polychæta may be briefly expressed as follows: The Polychæta—and with them the Annelida in general—have had for their ancestor a *non-metameric form of which the Trochophore is the larval representative, and this in the course of its development elongated, the elongation being accompanied by the repetition by a budding process of certain organs, a high grade of metamerization being thus produced.*

The relationships of the Trochophore seem to be with the Turbellaria. The nervous system, consisting of the apical thickening and lateral nerve-cords, is very similar to that of Turbellaria, and also it is interesting to notice the similarity of structure of the head-kidney with the Turbellarian nephridium. The exceedingly small development of the parenchyma is probably a secondary condition, and the presence of an anus is an important advance upon the Turbellaria. An undoubted similarity in many respects exists between the Rotifera and the Trochophore, and the former have been regarded as persistent Trochophores or else as forms descended from the Trochophore. This latter view in one of its phases has already been considered (p. 195), and an important difference in the relation of the supraœsophageal ganglion to the prototroch mentioned. Reasons have also been given for the belief that the Rotifera are descended from Turbellarian ancestors, and it seems probable that the line of descent of the Rotifers was identical for a time with that followed by the Trochophore, the former group branching off from it shortly before the Trochophore ancestor made its appearance on the scene. In this respect the Rotifers and the

Trochophore are related to each other, but hardly with so close an affinity as would be implied by a statement that they are persistent Trochophores.

II. Subclass **OLIGOCHÆTA.**

The Oligochæta are with few exceptions fresh-water or terrestrial Chætopods, and present a much simpler body form than do the Polychæts. The first segment or *prostomium* (Fig. 103, *pr*) is devoid of tentacles or cirri, and only in a few forms are eyes present upon it. The body is divided into well-marked segments, but parapodia are lacking, though in the majority of forms setæ, arranged in a more dorsal (*s'*) and a more ventral (*s*) group, occur on the sides of each metamere; in a few forms, however, a single series of groups only is present, while in *Perichæta* the setæ are arranged in a ring around each metamere, and in *Anachæta* they are wanting, their place being indicated only by the sacks in which in other forms they are developed and which project into the cœlom as large hypodermal glands. As a rule, too, no branchiæ are present, the blood being aerated through the walls of the body, minute branches of the blood-vessels penetrating into the hypodermis in the terrestrial forms; a few aberrant forms, however, possess either dorsal or ventral (*Chætobranchus*) appendages, which are probably respiratory in function, on many of the segments, while in the genus *Dero* the finger-like processes of the terminal metamere are probably branchiæ.

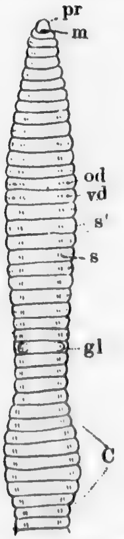


FIG. 103.—ANTERIOR END OF *Lumbricus*

C = clitellum.
gl = glands.
m = mouth.
od = opening of oviduct.
pr = prostomium.
s = ventral setæ.
s' = lateral setæ.
vd = opening of vas deferens.

The exterior of the body is covered by a well-marked cuticle, and beneath it lies the ectoderm or *hypodermis*, usually rich in gland-cells and also containing numerous sensory cells connected at their inner ends with slender fibrils which pass centrally and unite with others to form nerve-cords passing to the ventral nerve-cord. In some of the segments near the anterior portion of the body the hypodermis is usually thicker than elsewhere and richer in gland-cells, forming a structure known as the *clitellum* (Fig. 103, *c*). Within the hypodermis is a usually thick layer of circular muscles, and, internal to this, longitudinal muscles whose continuity as a layer is interrupted at the dorsal and ventral mid-lines as well as at the sides. Muscular dissepiments divide the cœlom into compartments corresponding to the external segmentation of the body, and the various compartments are lined by a layer of peritoneal cells which along the dorsal and ventral lines is reflected towards the digestive tract, which it surrounds, forming a dorsal and ventral mesentery. The former of these frequently disappears, as may also the ventral one. The dissepiments are rarely perfect, being usually perforated so that the various cœlomic compartments are placed in communication with each other, and in rare cases a number of the dissepiments may be wanting, as in *Æolosoma*, where but a single one separating the head from the trunk cœlomic spaces occurs. On the median dorsal line of more or fewer metameres towards their posterior edge a small opening usually occurs, the *dorsal pore*, and similar pores are found in the head segment of some forms. They place the cœlomic cavity in communication with the exterior, but do not seem under ordinary circumstances to be the means of any extensive interchange between the external water and the cœlomic hæmolymph, though occasionally this latter fluid may find exit through them. Among the peritoneal cells are usually to be found some which enclose greenish-brown particles and may detach themselves from the peritoneal layer and float about in the hæmolymph, eventually dying and disintegrating. Occasionally these *chloragogue cells* are specially aggregated in a furrow which runs along the dorsal surface of the intestine, and immediately surround the dorsal blood-vessel. They seem to be excretory in function, performing perhaps to a certain extent the part of the liver-cells of the Vertebrata.

A circulatory system is always present, and consists of a dorsal longitudinal vessel lying on the dorsal surface of the digestive tract and a ventral one lying below it, the two being united in more or fewer of the metameres by one or two lateral vessels on each side. The dorsal vessel is contractile, the blood in it flowing towards the anterior extremity, and the lateral vessels are also usually contractile. Branches are given off to the muscles and to the various organs in regular metameric succession, and additional longitudinal vessels are also found accompanying the ventral nerve-cord, two lateral and one ventral. In the terrestrial forms fine branches penetrate into the hypodermis, the aeration of the blood being thus effected in the absence of special branchiæ. The blood in the majority of forms is red from the presence of hæmoglobin dissolved in the plasma and contains colorless corpuscles. As in the Polychæta the cœlom contains a hæmolymph in which corpuscles float.

The digestive tract forms a straight tube, extending from the mouth, situated on the ventral surface at the junction of the prostomium and first trunk metamere, to the terminal anus. The mouth opens into a short mouth-cavity, and this into a more or less muscular pharynx, which in most cases can be protruded from the mouth and is slung to the body-wall by numerous radiating muscular bands. To it succeeds a smaller œsophagus, which communicates posteriorly in terrestrial forms, after in some cases dilating to form a sack-like thin-walled *crop*, with a muscular *gizzard*. The intestine which succeeds this is usually somewhat pouched, being constricted in the region of the dissepiments and bulging out into the intervening cœlomic cavities. In the terrestrial Oligochæts its absorptive surface is increased by the projection into it along the dorsal surface of a longitudinal fold, the *typhlosole*, the chloragogue cells lying in the furrow produced by the fold. Various glands open into the digestive tract at different regions, as, for instance, salivary glands which open into the anterior part of the œsophagus in some forms, and calciferous glands (Morren's glands) which contain particles of carbonate of lime and are found opening into the œsophagus in terrestrial forms.

The nervous system consists of a supraœsophageal ganglion (Fig. 104, *ce*) of a somewhat complicated structure lying in the anterior portion of the body. In *Æolosoma* it is connected with the hypodermis (i.e., the ectoderm), but in most forms it lies upon the anterior part of the digestive tract, quite separate from the hypodermis. It differs in position from the corresponding ganglion of the Polychæta in that it is not usually situated in the anterior metamere or prostomium, but has passed farther back and may lie in the second, third, or fourth metamere or even more posteriorly. It sends off nerves to the sensitive prostomium and gives rise to two commissures which pass backwards and downwards on either side of the pharynx to unite with the subœsophageal ganglion (*so*), which, like the brain, is formed of two more or less fused lateral masses, each of which in many forms shows indications of being compound and formed by the fusion of two or more ganglia (*Lumbricus*). To this there succeeds in each metamere a pair of ganglia each of which is united to its predecessor and successor by a pair of connecting cords, the whole ventral cord (*n*) so produced having a characteristic ladder-like arrangement. Usually the connecting cords are closely approximated, and the same may be the case with the ganglion pairs, the whole being ensheathed in connective tissue so that the cord seems to be single. From each pair of ganglia in *Lumbricus* three nerves pass out on each side, the two posterior ones being closely related so as to appear to be one. Nerves especially connected with the digestive tract, the *stomatogastric nerves*, seem to be present, but their distribution and connections have not yet been thoroughly studied. In some aquatic forms a *lateral nerve* imbedded in the hypodermis and united anteriorly with the supraœsophageal ganglion runs along the lateral line between the two rows of setæ, recalling the lateral-line nerve of the *Capitellidæ* among the Polychæta.

Sense-organs of various kinds are present. Tentacles are absent throughout the group, and in only a few forms (*Nais*) do eyes, consisting of pigment-spots imbedded in the hypodermis, occur. Ciliated depressions at the side of the prostomial segment occur in *Æolosoma* and a few other genera, while tactile setæ or papillæ are scattered over the body. In those forms which possess a lateral nerve sense-organs resembling those of *Capitella* occur metamerically along it, and in the genus *Slavina* are increased in number so as to form a circle of from fifteen to twenty papillæ surrounding each metamere and innervated by a branch from the lateral nerve. Cup-shaped organs, supposed to be gustatory, occur especially abundantly on the prostomial metamere.

The excretory system has usually a typically metameric arrangement—a single pair of coiled tubules lying in each metamere. Each tube opens by a ciliated funnel into one cœlomic compartment and then passes backwards, perforating the dissepiment, into the next succeeding compartment in which the coiled portion lies, and opens to the exterior in this metamere between the dorsal and ventral rows of setæ. The lumen of the coiled portion of the tubule is intracellular, the tubule consisting in this region of a series of perforated cells recalling the condition found in the Platyhelminths. In a certain number of anterior metameres the nephridia may be wanting in the adult condition, though in younger stages provisional nephridia are to be found in these metameres later disappearing.

Considerable variation is to be found in the nephridial system of the Oligochæta, some of the variations suggesting important theoretical considerations. A *head-kidney* similar to that described as occurring in the Trochophore larva persists in the adult stage in some Oligochæta, and in *Ctenodrilus* appears to be the only nephridium which exists. In other forms, such as *Chætogaster*, the entire nephridial system is composed of tubules having a decided similarity to the head-kidney in the intracellular character of the lumen, and in the absence of any ciliated funnel, the inner end of the tubule being closed. Furthermore the cells enclosing the canal are in addition perforated by numerous minute branching canals which open into the central lumen. This fact suggests the complete homology of the nephridial system throughout the entire body notwithstanding the usual marked histological distinction between the head-kidneys and the nephridia of the trunk metameres. There seems little reason to doubt that the Oligochæta have been derived from the Polychæta, and the nephridial system in the two forms is, therefore, homologous. It must, therefore, be possible for a nephridium with an intracellular canal to be transformed into one in which the canal is intercellular. The nephridia of *Chætogaster* are unquestionably homologous with those of *Lumbricus*, for instance, which possess a terminal funnel, and are likewise similar in structure to and may be regarded as repetitions of the head-kidney, thus establishing the homology between the two forms of nephridium.

In carrying the homology of the Annelid nephridium back to that of the Platyhelminth the question arises whether it is equivalent to the whole branching system of the Turbellarian or only to a part of it. Whichever view of metamerism be taken the various nephridia of the Annelids are to be regarded as bud-products, and each, therefore, equivalent to a branching Turbellarian nephridium. It has been suggested that the Annelid nephridial system has been produced by the fragmentation of an originally continuous system, but for this there is no embryological evidence. Each nephridium being a bud from an undifferentiated nephridial blastema is just as much an organ-individual as is the branched nephridium of a Turbellarian—just as much an individual, though of a lower grade, as is the bud of a Polyzoon developed from an undifferentiated blastema. It might be supposed, then, that the Annelid nephridium might show a branched structure in certain primitive forms, and indeed a branched head-kidney occurs in Polychæt Trochophores. A branched condition is, however, rare in the trunk nephridia, though it does occur in certain terrestrial Oligochæta in which, however, it must be regarded as a purely secondary phenomenon without any phylogenetic significance, since in the development of such nephridia a single tube is first formed which later on becomes solid and then gives off the branches, the various nephridial branches of successive segments becoming sometimes united. This branched condition passes into one in which the various branches separate and acquire independent openings; several pairs of nephridia, four in the anterior segments of a species of *Perichæta* and a greater number in other forms, occurring in a single segment. This branching and multiplication of nephridia is confined to terrestrial forms which in their conditions of existence are farthest removed from the primitive state, and it is not improbable that the multiplication bears some relation to the assumption of a terrestrial mode of life. In the genus *Lumbricus*, in which the nephridia are simple coiled tubes, a duplication of the nephridia in some segments is to be found. The reproductive ducts are probably modified nephridia, and in all aquatic forms other nephridia are absent in the metameres in which they occur. In *Lumbricus*, however, in, for instance, the metamere which contains the oviducts, two pairs are present, one of which retains its original excretory function, while the other has been modified to form a duct for the reproductive elements.

The reproductive organs have a very different arrangement from what is found in the Polychæta, being limited to a comparatively few metameres; and furthermore the Oligochæta are throughout hermaphroditic, the male and female organs both lying in the anterior portion of the body, usually between the ninth and fourteenth metameres, or sometimes even farther forward. There are either one or two pairs of testes (Fig. 104, *t*), which arise like the ovaries from the peritoneal epithelium and early break down to a greater or less extent, their cells passing into seminal vesicles (*vs*), where they undergo further development into spermatozoa. The *vasa deferentia* (*vd*) are modified nephridia, and are either two or four in number according as there are one or two pairs of testes. When four are present they may open separately, or may unite in pairs on either side in a common atrium, through which they open to the exterior, or finally those of the same side may unite a short distance below the funnels, forming for the greater part of their course a single tube. There is only a single pair of ovaries (*ov*), to which in some forms ovarian receptacles similar to the seminal vesicles are added; and in all but some of the lower forms oviducts (*od*), which are modified nephridia, are present. In front of the metameres which bear the testes one, two, or occasionally three pairs of invaginations of the body-wall occur, producing pouches projecting into the body-cavity—the seminal receptacles (*rs*)—which receive the seminal fluid during the mutual interchange of it which takes place on copulation.

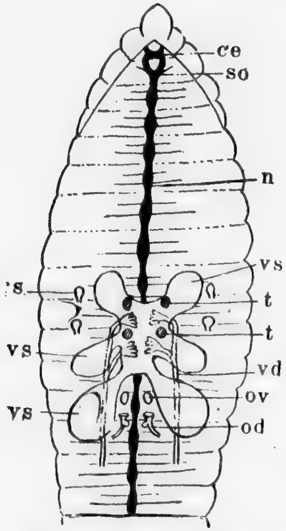


FIG. 104. — NERVOUS SYSTEM AND REPRODUCTIVE ORGANS OF *Lumbricus*.

ce = supracœsophageal ganglion.
n = ventral nerve-cord.
od = oviduct.
ov = ovary.
rs = receptaculum seminis.
so = subœsophageal ganglion.
t = testis.
vd = vas deferens.
vs = vesicula seminalis.

A satisfactory subdivision of the Oligochæta into orders has not yet been possible; indeed the various families are so related to one another that such a subdivision seems unnecessary. Formerly it was the custom to recognize two orders, *Limicolæ* and *Terricolæ*, aquatic forms being referred to the former, and terrestrial ones to the latter—a division, however, which is decidedly artificial. Less so, but still unsatisfactory, is a division into *Naidomorpha*, reproducing non-sexually, and *Lumbricomorpha*, reproducing by the sexual method only. It seems on the whole better to omit a subdivision into larger groups, and recognize one into families only.

Development of the Oligochæta.—In the development of the Oligochæta there is practically no larval stage, but a sufficient amount of nutrition is supplied to the embryo, either in the form of yolk in the egg itself or as an albuminous substance stored up in the interior of a cocoon in which the ova are contained, to enable it to pass through all its early stages while still within the egg-shell or cocoon, and to assume a free life only when it has reached the form of the adult. The Trochophore larva under such conditions is useless, and is suppressed in the ontogeny, the development becoming thus *direct* or of the *fœtal type.* This mode of development has been acquired as an adaptation to the aquatic or terrestrial life, in which, for obvious reasons, the occurrence of a free-swimming larva would be an inconvenience rather than an advantage.

In the Polychæta it was stated that usually at a very early stage of development one cell, later dividing into two, differentiates from the rest as the primary mesoblast, and gives rise to all the mesodermal tissues of the adult worm. This is an example of a *precocious segregation* of the mesodermal material into a single cell. It is to be presumed that in more primitive forms the mesoderm separated off from the endoderm only at a relatively late period of development; the tendency, however, for the appearance of an important structure to be thrown farther and farther back in the individual development, to appear at successively earlier stages in the development, has asserted itself to such an extent that the mesoderm in the Polychæta makes its appearance while the embryo is still composed of but a few cells, becoming therefore segregated in a single cell. Such a process has furthermore the advantage of permitting a rapid growth, the original embryonic mesoblasts retaining their position at the posterior end of the body and giving rise by division in a transverse plane to rows of cells, the mesoblast bands. Such a precocious segregation of the mesoderm also occurs in the Oligochæta. In a *Lumbricus* embryo there may be seen near the posterior extremity of the body the two mesoblasts (Fig. 105, *m*), lying one on each side of the middle line, with the mesoblast-bands (*mb*) extending forwards from them. A little in front of them and on either side may be seen another cell (*nb*), giving rise to a band extending anteriorly, which later on will become differentiated into the ventral nerve-cord, the cells which give rise to it being *neuroblasts;* while a little behind and externally to these, on either side, two other cells (*ne* and *x*) occur, giving rise likewise to germ-bands, whose further fate is undecided, though it seems probable that the inner of the two bands gives rise to the nephridia, the cells being *nephroblasts.* Thus from a small number of cells the entire nervous system, with the exception of the supraœsophageal ganglion (which arises as a local thickening of the ectoderm, comparable to the apical thickening of the Trochophore), the nephridia and all the other mesodermal tissues arise, the precocious segregation of these organs being carried to an extent only equalled in the Hirudinea. Indications of it, however, are found in the Polychæta, not only in the mesoblasts but also in a layer of cells occupying the ventral surface of the embryo, and forming the so-called *ventral plate,* from which the ventral nerve-cord, the nephridia, and some of the musculature seem to arise. A reduction of the number of cells constituting this ventral plate to the smallest number consistent with a bilateral symmetry, that is, to two for each

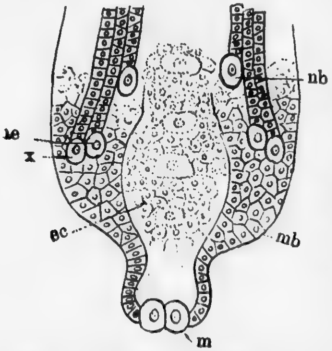


FIG. 105.—SURFACE VIEW OF POSTERIOR EXTREMITY OF EMBRYO OF *Lumbricus* (after E. B. WILSON).

ec = ectoderm.
m = mesoblast.
mb = mesoblast-band.
nb = neuroblast.
ne = nephroblast.
x = lateral teloblast.

set of structures formed from it, would give rise to a condition such as is found in the Oligochæta.

A number of the simpler Oligochæts, in addition to reproducing in a sexual manner, also reproduce by division, and in some forms it plays a much more important part than the sexual method, which in *Æolosoma* is not yet known to occur. In the simplest form of this method of reproduction the animal simply divides at the middle, each portion after separating regenerating the parts which are wanting. In one species of *Ctenodrilus* each metamere except the anterior one may separate and become a new individual; a phenomenon which might be regarded as illustrating the bud theory of metamerism, but which seems more properly to be a case in which the gradual integration of the multiplied organs has reached its highest development—the case standing as the culmination of the process of metamerization rather than as an example of its mode of origin. In *Nais* a division of the new individuals may begin before they have separated, and chains may thus be produced composed of individuals varying in the stage of regeneration which they have reached, but which eventually separate and may later become sexually mature.

As might be expected from the occurrence of this mode of reproduction, the power of regeneration of lost parts is possessed in a high degree by the Oligochæta; and not only in those forms which habitually reproduce by division, but also in forms like *Lumbricus*, in which under normal conditions this method of reproduction is unknown.

Affinities of the Oligochæta.—There is little reason to doubt that the Oligochæta have been derived from the Polychæta, and represent members of that subclass which have become specially adapted to aquatic or terrestrial modes of life. A few Oligochæts, such as *Halodrilus*, are marine, living below stones between tides; but they are undoubtedly derived from aquatic forms, and cannot be regarded as having any ancestral significance. As regards the more definite affinities of the group little can at present be stated with certainty. They have been referred to forms like the Capitellidæ, in some of which the parapodia are very much reduced, as is likewise the distinctness of the head, while, as in the Naids, lateral-line sense-organs are present. A more remote relationship through the Archiannelida has also been suggested, but at present no definite evidence is forthcoming as to which view is to be preferred.

II. Class **Hirudinea.**

The Hirudinea differ from the Chætopoda in their external form, being destitute either of parapodia or setæ, and possessing at the anterior end of the body a muscular sucker at the bottom of which the mouth is situated, while a second larger sucker used for attachment occurs at the posterior extremity of the body. The outer surface of the body is distinctly ringed, but a comparison of the rings with the internal organs shows that they have not a metameric value, but that a number of them, varying in different forms, are included in each true segment of the body. In *Branchellion* and *Clepsine* three such rings correspond to a metamere, in *Ichthyobdella* and *Pontobdella* six, in *Piscicola* twelve, and in all the group of the Gnathobdellidæ five. Towards the anterior and posterior ends of the body a reduction of the number of rings corresponding to a metamere is found, as for instance in the genus *Macrobdella* (Fig. 106), which has in the middle region five rings to a segment. The first two metameres consist of but one ring each, the third of two rings, the fourth, fifth, and sixth each of three rings. At the posterior end of the body the twenty-third metamere consists of four rings, the twenty-fourth, twenty-fifth, and twenty sixth of two rings each; while probably no less than seven metameres whose rings are not readily distinguishable are represented in the posterior sucker. The entire animal consists, therefore, of *thirty-three* metameres, and this number is characteristic for all the Hirudinea—a definiteness of number which contrasts strongly with the wide variations found in the Chætopoda. This number does not include a small lobe in front of the most anterior metamere, which may be equivalent to the prostomial lobe of the Oligochæta, and may represent another metamere.

As in the Oligochæta the gland-cells of the hypodermis at about the time of reproduction become enlarged and more abundant in a definite region of the body, forming a clitellum which is usually in the neighborhood of the tenth, eleventh, and twelfth metameres. As a rule no branchiæ occur, though an exception is found in the marine genus *Branchellion*, in which each ring of the middle region of the body bears an appendage which functions as a gill. In another marine form, *Pontobdella*, large warts occur on certain rings, which probably are mainly respiratory in function, being richly supplied with blood-vessels.

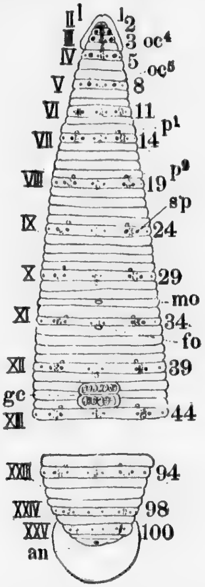
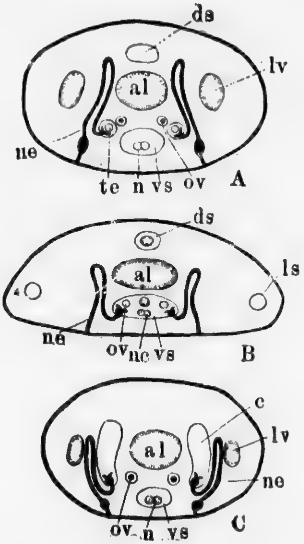

I 1
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
gc
XXIII
XXIV
XXV
an
1 2
3 oc⁴
5 oc⁵
8
11
14 p¹
19 p²
sp
24
29
mo
34
fo
39
44
94
98
100

FIG. 106.—ANTERIOR AND POSTERIOR EXTREMITIES OF *Macrobdella sestertia* (after WHITMAN).

an = anus.
fo = opening of oviduct.
gc = copulatory glands.
mo = opening of vasa deferentia
oc = eyes.
p = nephridial pores.
sp = sense-papilla.
1–100 = annuli.
I–XXV = metameres.


ds
lv
al
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C

FIG. 107. — DIAGRAMS TO SHOW ARRANGEMENT OF BLOOD-SINUSES OF (*A*) *Hirudo*, (*B*) *Clepsine*, AND (*C*) *Nephelis* (after BOURNE).

al = digestive tract.
c = cœlom.
ds = dorsal sinus.
ls and *lv* = lateral sinus or vessel.
n and *nc* = ventral nerve-cord.
ne = nephridium.
ov = ovary.
te = testis.
vs = ventral sinus.

The exterior of the body is covered by a cuticle, beneath which lies the hypodermis. The muscular tissue which underlies the hypodermis consists, as in other Annelida, of layers of longitudinal and circular fibres; and in addition, between these, a layer composed of fibres which cross one another obliquely is usually present. A marked distinction from what occurs in the Chætopoda is found in the cœlom, which in the Hirudinea is traversed by a parenchyma, recalling that of the Platyhelminths, so that the actual cavity is to a great extent obliterated and the dissepiments only to be distinguished with difficulty. Those portions of the cœlom which persist (Fig. 107, *Cc*) are occupied by a red or colorless fluid containing corpuscles and identical and continuous with that found in the blood-vessels. The cœlom is in fact represented by a number of blood-sinuses, which in some forms are lined by an epithelium, while in others such a lining is wanting. On account of the manner in which the blood-vessels anastomose with the sinuses it is exceedingly difficult to distinguish which spaces should be considered as belonging to the circulatory system proper and which to the cœlom—if, indeed, the two are to be considered fundamentally distinct. As a rule four main longitudinal vessels or sinuses are to be found—viz., one dorsal (Fig. 107, *ds*), which may be wanting (*Nephelis*, Fig. 107, *C*) and which probably corresponds to the dorsal vessel of the Chætopoda; one ventral (*vs*), sinus-like in character and frequently destitute of an epithelial lining, which surrounds the ventral nerve-cord; and two lateral vessels (*lv* and *ls*) unrepresented in the Chætopods, and perhaps also to be regarded as remnants of the cœlomic cavity. Communications between these longitudinal vessels occur through the medium of smaller vessels; and in some forms, such as *Nephelis*, the connection between the lateral and ventral vessels takes place through ampullæ, globular vesicles arranged in two pairs on each side of a number of metameres and receiving blood-vessels from the ventral sinus, while other vessels passing to the main lateral vessels arise from them. In many forms, especially among the Gnathobdellidæ, a rich plexus of capillary vessels penetrates the hypodermis.

The union of the blood vascular system with sinuses which most probably represent portions of the cœlomic cavity suggests an intimate relation, so far as its origin is concerned, of the vascular system with the cœlom; and this view is borne out by what has already been seen to occur in the

Nemerteans (p. 165), the lowest forms that possess a distinct blood vascular system. In this group the cœlom, so far as it exists, consists of small spaces without any definite walls scattered through the parenchyma. In some forms the blood vascular system communicates with these spaces through which the blood circulates, it being only in the most highly differentiated Nemerteans that the vascular system is closed. It might be supposed from this that the blood-vessels were simply cœlomic spaces which had acquired definite walls; and it seems probable that such has been their origin. In the Annelida a somewhat different state of affairs occurs. Here, as a rule, there is a definite cœlom lined with peritoneum and completely separated from the cavity of the blood-vessels, which seem to represent rather the remains of an original cavity, the so-called blastocœl (see p. 52), which has been almost obliterated by the growth of the mesodermal segments by the hollowing out of which the cœlomic cavities have been formed (see p. 56). It seems certain that the cœlomic spaces of the Nemerteans are likewise the remains of a primitive blastocœl, so that to this extent the homology of the blood-vessels holds in the two groups.

In the Hirudinea, however, the blood-sinuses, if they are cœlomic, correspond with the cœlom of the Polychæta ; and furthermore, in the Oligochæts and Polychæts, as well as in the Gephyrea, as will be seen later, the hæmolymph contained in the cœlom is very nearly if not quite identical in composition with the blood contained in the blood-vessels. These facts would seem to indicate a close relationship between the Annelid cœlom and the more primitive blastocœl; or, in other words, would lead us to suppose that the cœlom of the Annelids lined with peritoneum is not something apart and distinct from the blastocœl cavity, as has usually been supposed. The view which maintains the distinctness of the two forms of cœlom has its origin in the fact that in some forms, such as *Sagitta*, a cœlom lined with peritoneum is formed as an outgrowth from the primitive digestive tract; and it was supposed that all cœlomic cavities with definite walls were primarily of a similar origin, and hence were termed *enterocœls* in contradistinction to the *schizocœls* or simple spaces in the mesoderm without definite walls, which are in reality remnants of the blastocœl. The significance of true enterocœls will be discussed later. In the mean time it may be pointed out that there is no embryological evidence in favor of the Annelid cœlom having arisen as a series of pouch-like outgrowths from the primitive digestive tract. It is rather to be regarded as a schizocœl whose character has been altered by metamerization, and by the manner of its formation from mesoblasts. On this view the union of the cavity of the blood-vessels with the cœlom in the leeches, and the similarity of the hæmolymph to the blood in other forms, cease to be morphological puzzles.

The mouth lies at the bottom of the anterior sucker and opens into a muscular pharynx, which in some forms (e.g. *Clepsine*) is folded similarly to that of some Turbellaria (see p. 134) so as to form a protrusible tube, while in others (e.g. *Hirudo*,

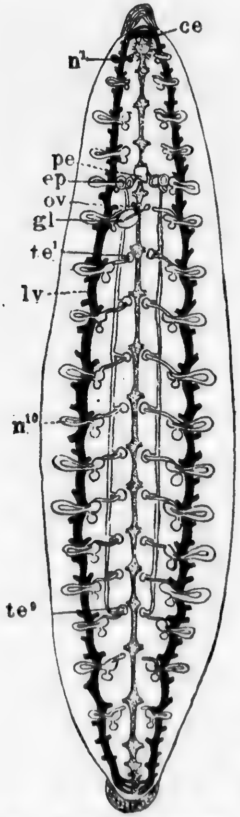

Fig. 108.—Diagram of the Excretory Reproductive and Nervous Systems of *Hirudo* (after Bourne).

ce = cerebral ganglion.
ep = epididymus.
gl = oviducal gland.
lv = lateral blood-vessel.
n = nephridia.
ov = ovary.
pe = penis.
te = testis.

Macrobdella) it is thrown into three longitudinal muscular ridges whose edges may become converted into chitin, thus forming teeth. Salivary glands open into the pharynx in some forms. The large stomach into which the pharynx opens behind gives off a number of lateral pouches (eleven pairs in *Hirudo*, seven in *Clepsine*), sometimes branched and increasing in size from before backwards, the most posterior pair being usually quite long and directed backwards parallel to the straight narrow intestine which opens to the exterior on the dorsal surface of the body, just anterior to the posterior sucker. Occasionally only the posterior pair of pouches is present, and in a few forms they are entirely wanting.

The nervous system (Fig. 108) is constructed on the typical Annelid plan. It consists of a circumœsophageal ring and a ventral nerve-cord composed of fibres which have their origin in ganglion-cells grouped together at definite intervals into ganglionic masses. Several of these ganglionic masses correspond to single segments, but at the anterior and posterior extremities a considerable amount of fusion of the metameric groups of ganglia has occurred. In *Clepsine plana* the portion of the nervous system which lies above the œsophagus consists of a transverse band of fibres passing laterally into the circumœsophageal commissures and of a number of ganglionic masses. Six of these latter lie in front of the band of fibres and correspond to the metamere formed by the prostomial lobe. Behind the transverse band are four additional ganglionic masses, apparently forming with the other six the supraœsophageal ganglion, but in reality forming together with two additional masses on the ventral side of the nerve-cord below the œsophagus the ganglion of the second somite. Immediately posterior to the two ventral masses is a chain of eight ganglia lying one behind the other on the mid-ventral line of the cord, and corresponding to these there occur on each side along the dorsal surface of the cord other eight masses, between each successive pair of which a nerve passes out. There are therefore four metameric ganglia represented in this complex structure, each consisting of six ganglionic masses and each giving rise to a pair of nerves. The subœsophageal ganglion accordingly consists of the ganglia of four metameres, to which must be added the two ventral masses of a fifth metamere, the supra- and subœsophageal ganglia representing together six metameric ganglia. Behind the subœsophageal ganglionic aggregate there lie twenty-one ganglia separated at some distance from each other, especially anteriorly, each one representing a metamere; and finally at the posterior end of the body is another ganglionic aggregate, representing, to judge from the number of nerves arising from it, seven metameric ganglia. Thus there are in all thirty-three, or, counting the ganglion which innervates the prostomium, thirty-four, metameric ganglia—numbers exactly corresponding with those obtained by counting the rings.

The sense-organs of the Hirudinea have especial interest as showing an adaptation of what may be considered tactile sense-organs to a different purpose. On each metamere of the body in all Hirudinea, with a few possible exceptions, small sensory papillæ (Fig. 106, *sp*) are to be seen, arranged in definite lines. They occur in the majority of forms on the first ring of each segment, though in some species of *Nephelis* they occur on all the rings. On the dorsal surface of each sensory ring there are three papillæ on each side of the middle line, and the same arrangement occurs on the ventral surface, and in addition a single papilla is found at the margin of the ring on each side. There are thus fourteen longitudinal rows of papillæ, six on the dorsal surface, six on the ventral surface, and two marginal. In the anterior and posterior segments whose width is reduced the marginal papillæ may be wanting, but throughout the rest of the body the number of rows is constant. In structure these papillæ are somewhat complicated, consisting of an axial bunch of elongated sensory cells bearing fine cilia at their outer ends, and lying in the connective tissue in their immediate vicinity is a varying number of large cells, each containing a large watery vacuole in the interior, the nucleus, in consequence, being pushed to one side. A strong nerve runs to each papilla and is supplied to the large vacuolated cells as well as to the axial sensory cells.

Slight differences are to be found in various forms in the structure of these organs. In *Clepsine* there is an axial bunch of hair-bearing cells to which the terminal fibres of the nerve run, and posteriorly and below the nerve are found the large vacuolated cells. In *Hirudo* and *Nephelis* no hair-bearing cells occur, the nerve occupying the axis of the organ and the vacuolated cells being arranged symmetrically around it.

It is probable, in view of the two kinds of constituent elements in *Clepsine*, that in this and similar genera a double function is possessed by the sensory papillæ, the hair-bearing cells having perhaps a tactile function, while the vacuolated cells are visual. It seems probable also that primarily the papillæ were similar in structure and function to the organs of the lateral line of certain Polychæta, such as the Capitellidæ, or perhaps it would be better to compare them with the tactile papillæ of certain aquatic Oligochæta, which in the genus *Slavina* have an arrangement on each metamere recalling that found in the Hirudinea.

Towards the anterior extremity of most of the Hirudinea a varying number of eyes are found. In some species of *Clepsine* but two such organs occur, while in others there are six, and in *Hirudo*, *Macrobdella* (Fig. 106, *oc*), and allied forms there are always ten. In the latter forms the eyes are always arranged in a definite manner: one pair is situated on the anterior ring (when more than one ring occurs) of each of the five metameres immediately following the prostomial lobe, and if their position be determined it will be found that they occupy the place of one of the dorsal sense-papillæ, the eyes being serially homologous with the sense-papillæ of one of the dorsal rows. This conclusion is verified by their structure, since they differ from the sensory papillæ only in the greater number of the large vacuolated cells and in the presence of a quantity of black pigment in the surrounding tissues.

Other sense-organs somewhat beaker-shaped in character are found upon the prostomium and have been regarded as gustatory in function.

Nephridia occur in a number of the metameres of the middle portion of the body, there being in *Hirudo* (Fig. 108, *n*) and its allies seventeen pairs. Each nephridium has a terminal funnel, which in *Clepsine* has the typical Annelidan structure, but in *Hirudo* has been modified so that the inner extremity of each nephridium is constituted by a lobed spongy ciliated mass without any definite central lumen. The funnel lies in a blood-sinus, either the ventral one as in *Clepsine* (Fig. 107, *B*) or the dorsal as in *Pontobdella*, or in a sinus which surrounds the testes as in *Hirudo* (Fig. 107, *A*), or in a special sinus which is to be regarded as a cœlomic space as in *Nephelis* (Fig. 107, *C*). The canal which traverses each nephridium is intracellular as in the Oligochæta, and in some forms minute canals traverse the substance of each cell, opening into the central lumen. As a rule the various nephridia are quite separate and distinct from each other, but in *Pontobdella* and one or two other genera they unite to form a network of intracellular canals traversing several metameres. Immediately before their exit to the exterior the canals enlarge in some forms to bladder-like vesicles, from which a short tube leads to the exterior, the opening being situated either upon the anterior (*Clepsine*) or the posterior (*Hirudo*) ring of the metamere to which the nephridia belong.

The reproductive organs differ from those of the Chætopoda in possessing ducts which do not seem to be modified nephridia and which are continuous with the walls of the ovaries or testes. All the Hirudinea are hermaphroditic. The ovaries constitute in *Clepsine* two elongated organs which lie in the middle region of the body, extending through several metameres, but in *Hirudo* (Fig. 108, *ov*) they are small oval or spherical bodies; their ducts dilate to form a uterus and finally unite to open on the mid-ventral line usually in the eleventh metamere (Fig. 106, *fo*). The testes (Fig. 108, *te*) consist of a number of pairs, varying from twelve or more to six (*Clepsine*), of spherical bodies lying in the same region of the body as the ovaries. Each testis has its own duct, which opens into a longitudinal vas deferens common to all the testes of the same side of the body. Anteriorly the two vasa deferentia unite to open in the mid-ventral line of usually the tenth metamere (Fig. 106, *mo*), frequently through a strong muscular penis (Fig. 108, *pe*). In many forms special glandular thickenings, supposed to be useful in copulation, occur on the ventral surface of one of the metameres behind that bearing the opening of the oviduct (Fig. 106, *gc*).

The Hirudinea are at present usually divided into two orders, though it seems probable that further division of one of them will be necessary later.

1. Order **Gnathobdellidæ.**

In this order are included the leeches which are provided with chitinous jaws in the walls of the muscular pharynx. In addition to this all the members of the order are characterized by possessing five rings to each fully developed metamere. To this order belong the Hirudinidæ, characterized by possessing ten eyes arranged in pairs on the five anterior metameres behind the prostomium, and including *Hirudo*, the medicinal leech, a native of Europe, instead of which *Macrobdella* is sometimes used in America. The Nephelidæ, with the genus *Nephelis*, differ in possessing fewer eyes (four pairs), and in having distinct segmental sense-organs either wanting or occurring on all the rings of each segment.

2. Order **Rhynchobdellidæ.**

The Rhynchobdellidæ are characterized by possessing a protrusible pharynx, as well as by possessing three, six, or twelve rings to a metamere. In the Ichthyobdellidæ, or fish-leeches, the larger numbers are found, the number six being characteristic of *Pontobdella*, while twelve occurs in *Piscicola*. In the Clepsinidæ but three rings are found to each metamere, and the eyes are either two or six in number. To this family belongs the genus *Clepsine*, a common fresh-water form, as well as the tropical land-leech, *Hæmenteria*.

Development of the Hirudinea.—The Gnathobdellidæ deposit their eggs in chitinous cocoons, as do the Oligochæta, and the development is of the fœtal type, in contradistinction to the larval, the ova containing as a rule a considerable amount of yolk. The mode of oviposition of the majority of the Rhynchobdellidæ is unknown; but in the genus *Clepsine* the eggs are fastened to the ventral surface of the body of the parent, where they undergo development. This resembles closely the development of *Lumbricus*, allowing for the greater amount of yolk which is usually present. The same precocious segregation of mesoderm, nervous system, and nephridia in special budding cells, the mesoblasts, neuroblasts, and nephroblasts, is likewise found, and in later stages the mesoblast is distinctly segmented and cœlomic cavities are present, which later become to a great extent obliterated.

The Affinities of the Hirudinea.—It is exceedingly probable that the ancestors of the Hirudinea were to be found in the Oligochæta, the two groups having not a few structural features in common. The embryological peculiarities found in the two groups are strikingly similar; and furthermore the aquatic or terrestrial habits are not a little suggestive, for although some leeches are marine, nevertheless the majority are aquatic and a few terrestrial. The complete disappearance of parapodia may be considered a further development of the tendency towards their obliteration in the Oligochæta, where only the setæ are present, these even having disappeared in the Hirudinea in consequence of the development of the suckers and a new mode of locomotion. The suggestive arrangement of the sense-papillæ of the Oligochæte *Slavina* has already been mentioned.

It must not be forgotten, however, that the differences between the two groups are many and important. Such are, for instance, the disappearance of the original cœlomic spaces, the communication of the blood vascular system with sinuses, and the occurrence of special ducts for the reproductive organs. These differences have, however, equal or even greater importance when the attempt is made to trace the Hirudinea directly to the Polychæta, and it seems more satisfactory at present to refer them back to the Oligochæta.

III. CLASS **Gephyrea.**

The Gephyreans constitute a group of marine worms which differ from the Chætopoda principally in the more or less complete absence of metamerization. All trace of it is absent upon the outside of the body; for although the thick cuticle may be marked by distinct rings, these bear no relation to the internal parts and are, as in the Nematoda, due simply to the thickness of the cuticle. All traces of parapodia are lacking in many forms, while in others they are represented only by a pair of setæ situated on the ventral surface of the body, nearer the anterior than the posterior end. The body-wall presents a close similarity in its structure to that of the Chætopods—differing, however, in the occurrence of a more or less pronounced layer of fibres having an oblique direction. The cœlom is lined by a layer of flat peritoneal cells, but shows no division into more or less distinct compartments, no trace of metamerism, but, as in the Chætopods, the peritoneal lining is reflected upon the walls of the digestive tract, forming mesenteries suspending the intestine. As a rule the dorsal mesentery disappears, and in some cases the ventral one is almost wanting, the intestine being slung only by a number of irregular strands of connective tissue extending from it to the body-wall. In some forms (*Sipunculus*) the surface of the peritoneum, especially that covering the intestine, is dotted with numerous irregularly scattered minute depressions, whose openings are guarded each by a peculiar ciliated cell, and which contain cells comparable in function to the chloragogue cells of the Chætopoda. The cœlomic cavity is occupied by a hæmolymph, which in some cases is colored, and contains numerous cell-elements, some of which may be circular in outline and colored by hæmoglobin, while others are amœboid and colorless.

A blood vascular system, principally developed in the anterior portion of the body, is present and appears to be completely closed, though connections with the cœlom are said to exist in some forms. In *Sipunculus*, for instance, the system consists of a collar surrounding the œsophagus, sending branches into the tentacles which surround the mouth, and dorsally dilating into a wide sinus lying just below the brain; and from this sinus a dorsal vessel (Fig. 109, *Bs*) passes backwards along the digestive tract for a short distance, ending blindly where the œsophagus joins the stomach. In *Echiurus* a ventral vessel runs the entire length of the body just above the nerve-cord, and it is united with the dorsal vessel by lateral vessels at its anterior and posterior extremities.

The digestive tract may be either straight (*Priapulus*) or considerably convoluted (*Echiurus* and *Sipunculus*, Fig. 109, *Int*), and the anus is in some forms terminal (*Echiurus*), while in others the intestine bends upon itself and passes forward to open on the dorsal surface near the anterior end of the body (Fig. 109, *A*). Throughout the greater extent of the intestine there runs along its ventral surface a ciliated groove which is no doubt homologous with the accessory intestine of certain Polychæta (see p. 207).

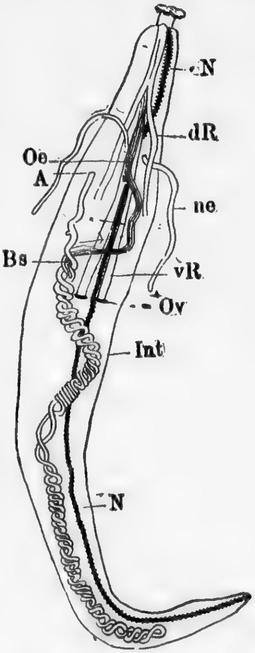

FIG. 109.—STRUCTURE OF *Sipunculus Gouldii* (after ANDREWS).

A = anus.
Bs = blood-vessel.
dR = dorsal retractor muscle.
Int = intestine.
N = nerve-cord.
ne = nephridium.
Oe = œsophagus.
Ov = ovary.
vR = ventral retractor muscle.

The nervous system partakes of the absence of distinct metamerism which characterizes the other parts. It consists of a brain lying in the anterior portion of the body above the œsophagus and sending a commissure downwards and backwards on each side to form the circumœsophageal collar. These two commissures unite to form a single nerve-cord (Fig. 109, *n*) extending the entire length of the body in the ventral median line, differing from the ventral cord of the Chætopoda in the absence of ganglia. Nerve-cells are scattered along the entire length of the cord and are not aggregated into special ganglia, though slight indications of such an aggregation are found in *Priapulus*. Nerves are given off at more or less regular intervals on either side, a somewhat metameric appearance being thus produced, but the corresponding nerves of opposite sides do not invariably arise from the cord opposite each other.

One, two or three pairs of nephridia (Fig. 109, *ne*) are as a rule present and form conspicuous brown tubes, which communicate by a funnel with the body-cavity at one extremity and with the exterior of the body at the other. They are undoubtedly homologous with the nephridia of the Chætopoda, possessing the same relations. In a few forms (*Bonellia*, *Phascolion*) a single nephridium only is present. In addition to these in *Echiurus*, *Thalassema*, and allied genera there is a usually much-branched organ on either side lying in the body-cavity and opening into the terminal portion of the intestine. Numerous ciliated funnels occur upon the branches placing the organ in communication with the body-cavity. This so-called "respiratory tree" (so named from a supposed homology with the similarly named organs of the Holothuria (q. v.) are probably nephridia, though whether or not they perform excretory functions is not quite clear. In *Priapulus* these organs are represented by branched tubes, the branches of which terminate blindly in flame-cells, resembling thus the excretory organs of the Platyhelminths, and in *Sipunculus* rudiments of these organs have been described as short tubes.

The Gephyrea are bisexual, the reproductive organs (*ov*) forming small digitate, elongate, or ovoid processes arising from the peritoneal lining of the body-cavity; but in some forms (*Sipunculus*) their products early escape into the cœlomic cavity, in which they float. The exact manner in which the ova and spermatozoa escape to the exterior has not been definitely ascertained for the majority of forms, but it seems probable that the nephridia serve as the generative ducts. In *Priapulus* the "respiratory trees" are said to give rise to the reproductive organs, and also to serve as the reproductive ducts—a behavior which would render exceedingly probable the supposition that they are modified nephridia.

Two orders are recognizable in the Gephyrea.

1. Order **Echiureæ.**

The Echiureæ, sometimes known as the *Gephyrea armata*, are characterized by the presence on the ventral surface of the body, in front of the openings of the nephridia, of a pair of setæ—the genus *Echiurus* possessing, in addition to these, two circles of setæ at the posterior extremity of the body. The anus is terminal in all the known species, and the terminal portion of the intestine has opening into it the branched respiratory trees. The anterior end of the body is prolonged into a prostomium of considerable size overlying the mouth; it may be short and broad as in *Echiurus*, more elongated and slender as in *Thalassema*, or deeply bifurcated at the extremity as in *Bonellia*.

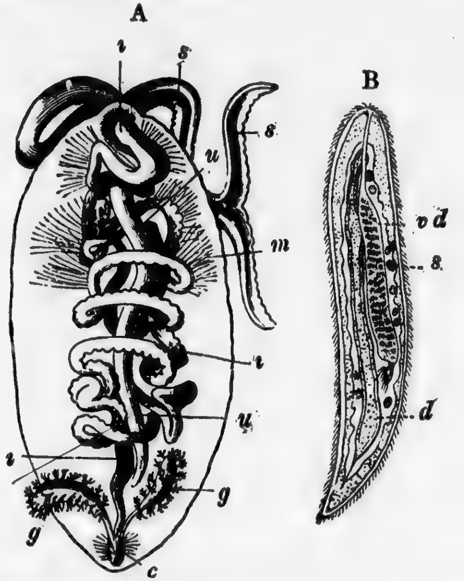

FIG. 110.—*Bonellia viridis A*, ADULT FEMALE OPENED SO AS TO SHOW THE PRINCIPAL ORGANS; *B*, male much enlarged in proportion to the female (from HERTWIG).

c = cloaca
d = rudimentary intestine.
g = respiratory trees.
i = intestine.
m = muscles.
s = proboscis.
s (in Fig. *B*) = spermatozoa.
vd = vas deferens.
u = single nephridium which serves also as the oviduct.

The last-named genus is interesting as affording an example of sexual dimorphism, the males being small Turbellarian-like organisms which live parasitically in the anterior portion of the digestive tract of the female, only coming to the exterior for the purpose of copulation.

2. Order **Sipunculacea.**

The Sipunculacea, to which the term *Gephyrea inermes* is also applied, is an order including forms which lack all traces of setæ. In *Priapulus* the intestine is almost straight and the anus terminal; but in *Sipunculus* and the allied genera, such as *Phascolosoma* and *Phascolion*, the digestive tract is convoluted and bent back upon itself, so that the anus lies on the dorsal surface near the anterior extremity of the body. A "respiratory tree" is absent or rudimentary as a rule except in *Priapulus* and allied genera, and the large prostomial lobe characteristic of the Echiureæ is lacking. The anterior portion of the body, however, is capable of being invaginated by means of strong retractor muscles (Fig. 109, *dR* and *vR*) into the fore part of the digestive tract, forming the so-called *introvert*. The extremity of this is provided with a circle of finger-like or branched tentacles in the centre of which lies the mouth, and which are supposed to have a respiratory function, being richly supplied with blood. In *Priapulus* these are absent, but at the posterior end of the body there is a prolongation which bears papilla-like processes which probably function as respiratory organs.

Development and Affinities of the Gephyrea.—The early development of the Gephyrea resembles closely that of the Polychæta, more especially in the Echiureæ. In this order a Trochophore larva is formed resembling very closely the typical Polygordius trochophore, the similarity extending even to a segmentation of the primitive mesoderm bands. In later stages this metamerism of the mesoderm disappears, no trace of it being found in the adult forms. In the *Sipunculacea* the larva differs from the Trochophore in lacking the typical præoral band of cilia, though this may be weakly developed in some forms, such as *Phascolosoma*. The postoral cilia are, on the other hand, strong. A further difference is found in the absence of metamerization of the mesoderm, which at a very early stage of development forms a layer lining the interior surface of the body-wall, and also covering the digestive tract and enclosing a cœlomic cavity continuous through the entire body.

Notwithstanding these important differences there seems little room for doubt but that the *Sipunculus* larva has arisen as an adaptation of the typical Annelidan Trochophore still represented in the development of the Echiureæ. By these forms a close relationship is shown to the Polychæta; and the Gephyrea are to be regarded as Polychæta which have secondarily lost a metamerization originally present in the adult ancestors and still represented in the *Echiurus* larva, but lost even in the larval stages of the *Sipunculacea*.

Since the discovery of the larval forms of certain Echiurid and Sipunculid forms there has been a tendency to regard these two orders as being much less closely related than they are here supposed to be. The Echiureæ are still held to have Annelidan affinities, while the Sipunculacea are assigned to the next type to be described. This tendency has its origin in the attachment of too great importance to the metamerism which is indicated in the Echiurid trochophore but lacking in the Sipunculid larva. There seems no good ground for supposing that its absence in the latter group may not be sufficiently explained by the assumption that it represents the final stage of the reduction of metamerism of which the transient segmentation of the Echiurid is a stage. In their anatomical characteristics the adult forms of the two groups are too much alike to be assigned to different types and the similarities of detail too numerous to warrant the belief that they have been independently acquired. It seems much more probable that both orders have descended from segmented ancestors—the degeneration, if degeneration it can be called, having been carried to a greater extent in the Sipunculacea than in the Echiureæ, and having in consequence been thrown back upon the larval stages and so obscuring the developmental evidences of the phylogeny.

A connecting link between the Echiureæ and the Polychæta has been traced by some authors in the genus *Sternaspis*, at one time associated with the Gephyrea but now universally assigned to the Polychæta. In this genus the metamerization, though to a certain extent reduced, is still pronounced, *S. arcuata* consisting of from twenty to twenty-two metameres, of which the anterior seven, together with the head-lobes, may be invaginated—the introvert of the Sipunculacea being thus recalled. On the ventral surface near the posterior extremity of the body are two shield-like plates armed with setæ, and at the posterior extremity, as in *Priapulus*, are a number of filamentous appendages which are regarded as branchiæ. Setæ are present on all the metameres except the fifth, sixth, and seventh; those of the eighth to the sixteenth metameres being, however, concealed beneath the hypodermis. The digestive tract is somewhat convoluted, but opens terminally; the ventral nerve-cord shows traces of ganglionic swellings, and at the posterior end of the body possesses a marked enlargement; and only two nephridia are present. The musculature and the vascular system resemble those of the Polychæta rather than those of the Gephyrea, while the reproductive organs are peculiar in possessing special ducts, which, it has been held, show no indications of being modified nephridia.

In many respects, accordingly, *Sternaspis* does hold a position intermediate between the Echiureæ and the Polychæta, and it seems not improbable that it may represent an offshoot from near the base of the line along which the Gephyrea have been differentiated. Whether this be the case or not, it is exceedingly probable that the Gephyrea have been derived from the Polychæta, the Echiureæ preserving more numerous traces of their ancestry than do the Sipunculaceæ.

IV. Class **Myzostomeæ**.

The Myzostomeæ constitute a group of Annelids which present but few traces of a typical metameric form, being much modified by their parasitic habit. All the known forms are parasitic upon Crinoids, some producing malformations of the pinnules of their host in the form of cysts in the interior of which they live. The body of *Myzostomum* (Fig. 111) is flattened and oval, a number of finger-like processes or cirri (*c*) projecting around the margin. There is no trace of external segmentation, although five pairs of parapodia (*p*), each with an axial supporting chitinous rod and a single hooked seta, occur on the ventral surface. On the same surface too, near the margin, are to be found in most species three or four sucker-like depressions (*su*) on each side, which have been supposed to represent highly-modified nephridia.

The body is covered by a thick cuticle beneath which lie the hypodermis and the musculature of the body-wall, which has the characteristic Annelidan arrangement. A body-cavity can hardly be said to exist (unless it be indicated by the space occupied by the ova), the interior of the body being completely filled up by the internal organs and by numerous muscle-bands passing both dorso-ventrally and from side to side, these latter in some forms being arranged in such a way as to represent incomplete dissepiments. There is no blood vascular system.

The mouth is situated near the anterior end of the body on the ventral surface and opens into the proboscis-sheath, within which lies the proboscis (*ph*), constructed upon the same plan as that of the Rhynchobdellid Hirudinea. Around the extremity of the proboscis are arranged a number of short tentacles, and its walls are very muscular; behind it opens through a short œsophagus into the wide intestine (*s*) from which three (or two) branched pouches project on either side towards the margin of the body. The short and relatively narrow rectum (*r*) opens near the posterior end of the body, uniting shortly before its termination with the oviduct.

The nervous system consists of a circumœsophageal commissural ring upon which lie numerous scattered ganglion-cells likewise surrounding the œsophagus and apparently representing the supraœsophageal ganglion. Numerous longitudinal nerves pass forward from the ring to unite with another ring around the base of the proboscis from which nerves pass to the tentacles. Below the intestine lies a large ganglionic mass with which the circumœsophageal commissures unite and which gives off a number of peripheral nerves. This mass is composed of several (probably 6) united ganglia and represents the ventral nerve-cord of other Annelids. Nerves pass presumably from the supraœsophageal ganglion-cells along the dorsal wall of the intestine and seem to constitute a sympathetic system. The only structures which can be considered sense-organs are the marginal cirri and the tentacles of the proboscis, which probably have a tactile function. No traces of eyes have yet been observed.

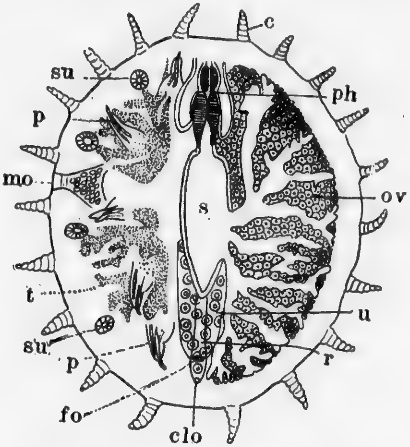

FIG. 111.—*Myzostomum* (after VON GRAFF).

c = cirrus.
clo = cloacal opening.
fo = opening of uterus into cloaca.
o = opening of male reproductive organs.
p = parapodium.
r = rectum.
s = stomach.
su = sucker.
t = testes.
u = uterus.
ph = proboscis.

Nephridia, unless they be represented by the sucker-like depressions and the oviducts, are wanting. The Myzostomeæ are as a rule hermaphrodite. It seems doubtful if the ovaries have actually been made out, the large masses of ova (*ov*) lying between the branches of the intestinal pouches, which have been considered ovaries, being more probably original cœlomic spaces which have become filled with ova set free from the ovaries; while the so-called uterus (*u*), lying immediately above the intestine, and which in mature animals is closely packed with ova, is probably of the same nature. Three oviducts, one dorsal and two lateral, pass from the uterus to open (*fo*) into the rectum near its termination, though the dorsal one in some forms may open directly to the exterior near the anus.

If the uterus is correctly identified as a cœlomic space, then it seems not improbable that the oviducts may represent modified nephridia. Their opening into the rectum is a secondary condition and does not necessarily stand in opposition to their nephridial character, since practically the same conditions obtain in some Rotifera.

The testes (*t*) are branched organs lying for the most part between the intestine and the nervous system, though isolated masses occur in some forms near the margin of the body. On each side two vasa deferentia, one anterior and one posterior, convey the spermatozoa to a muscular sperm-vesicle opening to the exterior at the margin nearly opposite the centre of the body (*mo*).

In some species, notwithstanding their hermaphroditism, "complemental males," small individuals which possess ripe spermatozoa while lacking ova, have been described as occurring. Further observations have not, however, tended to confirm this idea in its original sense, since these small individuals have been found to be, like the larger ones, hermaphrodites, being secondary adaptations from the prevailing hermaphroditic condition, and not having, therefore, the same significance as the "complemental males" of the Cirrhipedia (q. v).

There can be little room for doubt but that the Myzostomeæ are Annelida degenerated by parasitism, and that they are most closely related to the Polychæta. It is interesting to note in this connection the effect their parasitic and sessile mode of life under equable external conditions has had in producing indications of a radial symmetry.

APPENDIX TO THE TYPE ANNELIDA.

CLASS **PHORONIDÆ.**

The class Phoronidæ includes a single genus, *Phoronis*, of which but a few species are known. They are all marine forms of comparatively small size, reaching in some cases a length of 50 mm. Each individual is contained within a chitinous tube to which particles of sand are in some cases agglutinated, and is worm-like and cylindrical in form, the anterior extremity of the body being provided with a horseshoe-shaped fold, termed the *lophophore* (Fig. 112, *a*), bearing a number of tentacles arranged around its margins. Between the two circles of tentacles is situated the mouth (*b*), over which hangs a fold known as the *epistome*, representing the prostomium or præoral lobe of the larva. Outside the area enclosed by the tentacles is the anus, on either side of which a pore, the opening of a nephridium, is found.

The ectoderm of the body-wall is separated by a distinct basement-membrane from a layer of circular muscles, within which is a second layer of longitudinal muscles (*i*)—an arrangement resembling that found in the body-wall of the Annelids. Internally the longitudinal muscle-layer is lined by a layer of peritoneal cells enclosing a spacious cœlom. Near the anterior end of the body there is a transverse septum separating off, more or less perfectly, an anterior chamber, with which the cavity of the epistome and of the lophophore communicates, from a larger posterior chamber in which lie the intestine and reproductive organs, and which is divided longitudinally by three mesenteries extending from the intestine to the body-wall. One of these mesenteries accompanies the intestine throughout its entire extent, while the other two lateral mesenteries are in connection only with the sides of the descending limb of the intestine.

The tentacles are processes of the body-wall, with a ciliated ectoderm, and contain a chitinous axial supporting tissue.

A completely closed blood vascular system is present, consisting below the transverse septum of two longitudinal vessels (*h* and *f*). One of these (*f*) divides (*g*) near the anterior extremity of the body, the two branches passing into a circular vessel lying at the bases of the tentacles and sending branches up into them. The vessels which return the blood from the tentacles open into a second ring external to the first, and from it two vessels pass backwards and unite to form the second longitudinal trunk from which numerous cæcal pouches arise. All the vessels have contractile walls, and the blood which they contain possesses nucleated red corpuscles.

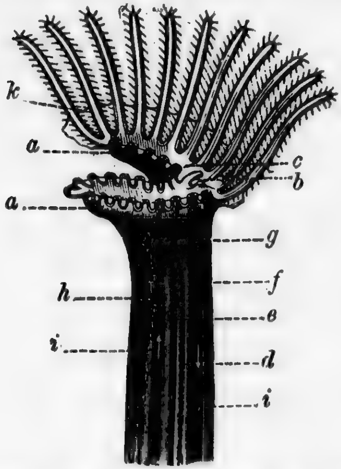

FIG. 112.—LATERAL VIEW OF ANTERIOR REGION OF *Phoronis* (after BOURNE).

a = lophophore.
b = mouth, surrounded by epistome.
c = lophophoral disk.
d = œsophagus.
e = intestine.
f = ventral blood-vessel.
g = branch of *f*.
h = dorsal blood-vessel.
i = longitudinal muscle of body-wall.
k = intertentacular membrane.

The digestive tract is bent upon itself (*d* and *e*), the mouth and anus, as already described, lying in close proximity at the anterior extremity of the body. Several regions, such as œsophagus, first stomach, second stomach, and intestine, are to be distinguished, and along one surface of the œsophagus and first stomach runs in *P. architecta* a ridge, becoming a groove in the stomach region, of ciliated gland-cells, which recalls the accessory intestine of the Gephyrea. There are no special digestive glands.

The nervous system is completely imbedded in the ectoderm. It consists of a nerve-ring, following the outline of the lophophore at the bases of the tentacles and surrounding, therefore, the mouth but not the anus. From it a nerve runs backward asymmetrically upon one side of the body to near the posterior extremity. It contains a large clear rod-like structure which seems to be a colossal nerve fibre.

The only sense-organs which have been described are a pair of ciliated depressions lying one on each side in the concavity of the lophophore; no definite statement can be made as to their function.

A single pair of nephridia is present, opening into the posterior chamber of the cœlom by funnel-like mouths, and to the exterior on each side of the anus. They serve not only for excretion, but also as ducts for the reproductive elements. The various species of *Phoronis*, with the possible exception of *P. architecta*, are hermaphrodite, the ova and spermatozoa developing from cells of the peritoneum lying in the vicinity of the pouched longitudinal blood-vessel. They are shed from their place of formation into the cœlomic cavity and thence pass to the exterior through the nephridia.

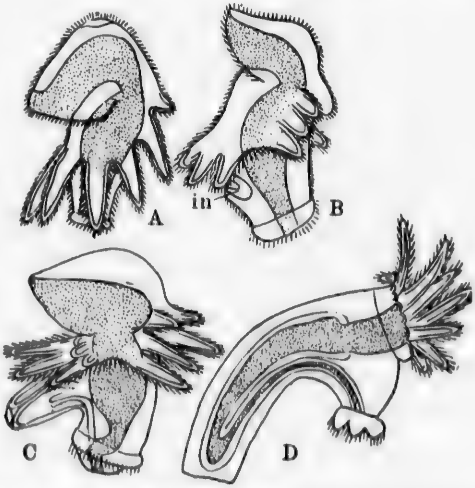

FIG. 113.—METAMORPHOSIS OF *Actinotrocha* (after METSCHNIKOFF from BALFOUR). *in* = invagination.

Development of the Phoronidæ.—In their development the various species of *Phoronis* so far as known undergo a very remarkable metamorphosis. The larva which develops from the ovum is known as *Actinotrocha* (Fig. 113, *A*) and is a somewhat elongated structure possessing at the anterior end a large hood which overhangs the mouth, its edge bearing strong cilia. Behind the mouth are a number of ciliated tentacle-like processes arranged in a horseshoe-shaped curve, their cilia, together with those of the edge of the prostomial hood, forming a band encircling the mouth. The digestive tract opens to the exterior at the posterior extremity of the body, and the axis of the body is the axis passing through the anus and the centre of the prostomial lobe. A little later (*B*) an invagination (*in*) of the body-wall into the cœlom of the larva develops on the ventral surface behind the band of ciliated processes and becomes of a considerable size. At the time of the metamorphosis this invagination is suddenly everted (Fig. 113, *C* and *D*), the intestine being carried with it as a loop, and entirely new axial relations are thus brought about. The long axis of the body is now (*D*) almost at right angles to what it was in the *Actinotrocha*, and since the invagination originally formed on the ventral surface of the larva, the body of the adult *Phoronis* must be regarded as formed by an excessive development of the ventral surface, the dorsal surface being represented only by the short interval between the mouth, or rather the epistome, and the anus. The epistome represents the prostomial lobe of the larva, and the ciliated processes represent the lophophoric region, though they themselves are afterwards replaced by the permanent tentacles.

There can of course be no question but that this remarkable metamorphosis is a secondary phenomenon, and it seems probable that its acquisition stands in relation to the tubicolous habits of the adult which necessitate the change of the principal axis of the body. The metamorphosis is the means of avoiding a slow and tedious change necessitated by the different habits of the larva and the adult, just as the occurrence of the chrysalis stage in the development of the butterfly is required on account of the great differences between the mouth-parts of the larval caterpillar and the adult butterfly.

The affinities of *Phoronis* cannot be considered to be finally settled as yet, though there has been a tendency of late years to associate them with the Polyzoa. They also seem to show affinities to the Gephyrea, and by some authors are considered more correctly referable to that group. The tendency to develop the ventral surface of the body at the expense of the dorsal and so to form a new body-axis is seen in *Sipunculus* and carried to its culmination in *Phoronis*, and further similarities between the two forms are to be found in the character of the nephridia and in the occurrence of a closed blood vascular system. The lophophore of *Phoronis*, and the epistome, are on the other hand characteristic Polyzoan features, and it seems not at all improbable that *Phoronis* occupies an intermediate position between the Gephyrea and the Polyzoa. There is this at all events to be noted concerning the Prosopygia (see following chapter), and that is that they are certainly closely related to the Annelida. If the supposition advanced on p. 243 to the effect that the Sipunculacea are to be regarded as Annelida which have secondarily lost their metamerism be correct, and if *Phoronis* really indicates a derivation of the Prosopygia from Gephyrean-like ancestors, then the Prosopygia too must be regarded as Annelida in which all traces of metamerism have been lost. This view seems preferable to that which would refer the Polyzoa, for instance, back to unsegmented ancestors—back, that is to say, to the non-segmented ancestors of the Annelida.

SUBKINGDOM METAZOA.

TYPE ANNELIDA.

I. Class CHÆTOPODA. — Metamerism usually well marked; with dorsal and ventral rows of setæ along the sides of the body.
  I. Subclass POLYCHÆTA.—Marine forms; with the setæ usually borne upon lateral lobes of the body (parapodia).
    1. Order *Archiannelida.*—Without parapodia. *Polygordius.*
    2. Order *Errantia.*—Elongated swimming or creeping forms; metameres more or less similar. *Nereis*, *Lepidonotus*, *Diopatra*, *Autolytus*, *Hesione*, *Syllis*, *Alciope*, *Capitella*, *Polyophthalmus*, *Arenicola*, *Aricia.*
    3. Order *Sedentaria.*—Usually tubicolous; anterior metameres more or less different from the rest. *Amphitrite*, *Serpula*, *Sabella*, *Terebella.*
  II. Subclass OLIGOCHÆTA.—Aquatic or terrestrial forms; with setæ, but without parapodia.
    1. Order *Naidomorpha.* — For the most part aquatic; frequently reproducing non-sexually; nephridia serve as reproductive ducts. *Nais*, *Dero*, *Chætobranchus*, *Æolosoma*, *Chætogaster*, *Ctenodrilus*, *Tubifex.*
    2. Order *Lumbricomorpha.* — For the most part terrestrial; not reproducing non sexually; special reproductive ducts. *Lumbricus*, *Perichæta*, *Anachæta.*

II. Class HIRUDINEA.—Metamerism well marked; without setæ; with anterior and posterior suckers.
    1. Order *Gnathobdellidæ.*—Mouth with three more or less well developed teeth; pharynx not protrusible. *Hirudo*, *Macrobdella*, *Nephelis.*

2. Order *Rhynchobdellidæ.*—Without teeth and with protrusible pharynx. *Clepsine*, *Pontobdella*, *Piscicola*, *Branchellion.*

III. Class Gephyrea.—Metamerism indistinct; without parapodia.

1. Order *Echiureæ.*—With setæ. *Echiurus*, *Thalassema*, *Bonellia.*
2. Order *Sipunculaceæ.*—Without setæ. *Sipunculus*, *Priapulus*, *Phascolosoma*, *Phascolion.*

IV. Class Myzostomeæ.—Parasitic on Crinoids; approximating a radial symmetry. *Myzostoma.*

APPENDIX.

Class Phoronidæ.—Without metamerism; tubicolous; with lophophore. *Phoronis.*

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CHAPTER XI.

TYPE PROSOPYGIA.

THE members of the type Prosopygia are compact, solitary, or colonial organisms destitute of a true metamerism and having the digestive tract usually bent upon itself, so that the anus lies in more or less close proximity to the mouth and therefore near the anterior end of the body. A chitinous or more or less calcareous investment is formed about the exterior of the body, and in some cases assumes the form of a calcareous bivalve shell, similar to that of the Pelecypoda in its general appearance, although in the relations of the valves to the body-surfaces and in other particulars (see p. 327) there are very decided differences, the similarity being simply an analogy.

A more characteristic feature, however, is the presence at the anterior end of the body of a circular or horseshoe-shaped fold, or else of two armlike lateral processes, forming what is termed the *lophophore*, upon which are borne a number of tentacles which play important rôles not only in obtaining food, but also in the process of respiration, no branchial or other special respiratory organs being present.

A more or less spacious cœlom is usually present, traversed by muscle-fibres and some specially developed muscle-bands, though the muscular system is on the whole poorly developed. The cœlom contains a hæmolymph, but a separate blood vascular system and heart is entirely wanting. The nervous system, in accordance with the absence of metamerism, is exceedingly simple, consisting either of a single ganglion, lying between the mouth and anus and sending off nerves to the various regions of the body, or else of a nerve-ring surrounding the œsophagus, with more or less distinct supra- and sub-œsophageal ganglionic enlargements. Special sense-organs are wanting.

A pair of simply-constructed nephridia are present in some forms, but in many a special excretory organ seems to be entirely wanting. Bisexuality is the usual arrangement, although in the Polyzoa hermaphroditism is of not unfrequent occurrence.

The great majority of the Prosopygia are marine in habitat, though a number of Polyzoa are inhabitants of fresh water. The type may be divided into two well-marked classes, the Polyzoa and the Brachiopoda.

I. Class **Polyzoa**.

The Polyzoa, a group usually spoken of by German zoologists as the Bryozoa, are almost without exception colonial organisms, forming encrusting, massive, or more or less dendritic masses composed of a large number of small individuals or *polypides*, each of which is enclosed within a chitinous or in some cases partially calcified investment, the zoœcium, from the mouth of which the anterior portion of the body bearing the lophophore may be protruded. This outer investment or *ectocyst* (Figs. 115 and 116, *ec*) is lined upon its interior surface by a layer of ectoderm-cells, within which is a delicate peritoneal lining, these two layers together constituting the true body-wall or *endocyst* (Fig. 115, *en*) practically destitute of muscle-tissue, though a sphincter is usually present at the mouth of the cup, which may thus be closed over the retracted polypide.

A more or less spacious cœlom (Fig. 115, *co*) is present in the majority of forms, containing a hæmolymph and traversed by a number of muscle-strands (*m*) which may be aggregated into special retractor bands; but in one order, the Endoprocta (Fig. 114), these are wanting and indeed the cœlom is reduced to a very small space between the body-wall and the digestive tract. This latter structure has the characteristic U- or Y-shaped form and presents but little differentiation into special parts, though an œsophagus, stomach, lined with glandular so-called liver-cells, and rectum may be distinguished. An anus (Figs. 115 and 116, *a*) is always present and may be situated either within or without the area enclosed by the lophophore. The nervous system is exceedingly simple, consisting of a single ganglionic mass (Figs. 114 and 115, *ce*) lying between the mouth and anus, nerves ramifying from it to the various parts of the body. The only sense-organs that have been detected are situated upon the free portions of the body, more especially on the lophophoral tentacles (*t*), and are represented by scattered ectodermal cells each of which bears a strong cilium and is in connection with a nerve-fibre; they have been assigned a tactile function, though it seems probable that they react to stimuli of various kinds and have a much more generalized function.

The arrangement of the excretory and reproductive organs varies considerably in different forms and may be more conveniently described in connection with the various orders.

1. Order **Endoprocta.**

This order contains but a small number of forms, which, with one exception, *Urnatella*, are marine in habitat. They all possess the power of reproducing by budding, colonies being thus formed, as in *Pedicellina*, *Ascopodaria*, and other genera with the exception of *Loxosoma*, in which the buds separate completely from the parent at a relatively early stage of their development. Each individual (Fig. 114) is a cup-shaped structure, prolonged posteriorly into a stalk (*st*) and upon the rim of the cup, which represents the lophophoral fold, or slightly below it on the inner surface, the tentacles (*t*) are arranged in a circle surrounding a depression, the vestibule, into which open both the mouth and the anus, the situation of the latter opening within the circle of tentacles having suggested the name given to the order. The tentacles can be coiled in a circinate manner, so as to lie completely

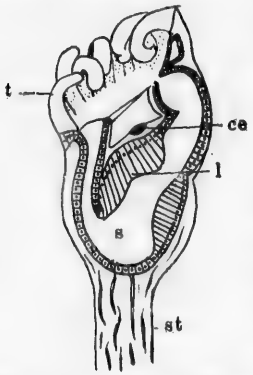


FIG. 114.—SINGLE INDIVIDUAL OF *Pedicellina* (after NITSCHE).
ce = ganglion.
l = so-called liver.
s = stomach.
st = stalk.
t = tentacles.

within the vestibule, and the rim of the cup can be closed over them, owing to the presence in it of a circular band of muscle-fibres.

The entire body is covered by a delicate cuticular ectocyst similar to the cuticle of the Annelids, below which is the ectoderm containing numerous gland-cells, as well as scattered sensory hair-bearing cells which, however, have not been found to exist in some genera (*Ascopodaria*). Scattered muscular fibres occur in the body-wall, but they do not as a rule reach an extensive development.

The cœlom is of very slight extent and in *Loxosoma* is replaced by a gelatinous matrix enclosing branching cells and muscle-fibres and recalling the parenchyma of the Turbellaria. Imbedded in this parenchyma is the U-shaped digestive tract, beginning with the mouth situated in the vestibule and overhung by a well-marked epistome. The mouth leads into a narrow œsophagus lined by ciliated columnar cells, and opening below into a saclike stomach (Fig. 114, *s*) which forms the lower transverse portion of the U. The cells of its anterior (vestibular) wall (*l*) are large and destitute of cilia, and contain numerous granules, on which account they have been termed "liver-cells." The intestine forms the ascending limb of the U, and like the œsophagus is ciliated, opening into the vestibule at the summit of a well-marked papilla.

The nerve-ganglion lies below the floor of the vestibule between the epistome and the anal papilla and is a single dumb-bell-shaped structure from which from one to three nerves arise on each side, branching to be distributed to the tentacles and muscles of the body.

A single pair of nephridia occurs, opening into the vestibule, and each is composed of a number of perforated cells, the lumen being ciliated. It is doubtful whether a flame-cell occurs at the inner extremity as in the Annelid head-kidneys, which otherwise they resemble. Most of the Endoprocta seem to be bisexual, though *Pedicellina* is perhaps hermaphrodite. The reproductive organs arise from the mesoderm of the body-wall, forming masses projecting into the parenchyma, and are provided with special ducts which either remain independent of each other (*Pedicellina*), or unite together to form a single tube and open into the vestibule, between the epistome and the ganglion.

2. Order **Ectoprocta**.

The order Ectoprocta includes the great majority of forms which are referable to the class Polyzoa. They are without exception colonial forms of small size in which the tentacles are arranged either in a circle or in the form of a horseshoe surrounding the mouth, the anus being invariably situated, contrary to the arrangement in the Endoprocta, outside the limits of the lophophore. The tentacles, too, when retracted are not flexed or coiled as in the Endoprocta, but are simply approximated to form a bunch, each tentacle being straight and parallel to its fellows.

The most characteristic peculiarity of the Ectoprocta, however, is the power which they possess of withdrawing or retracting the anterior portion of the body with its crown of tentacles within the posterior part (Fig. 115). This latter portion is enclosed in the *ectocyst* (*ec*) to which the body-wall is closely adherent and which forms a chitinous or, in some cases, more or less calcareous cell, termed a *zoœcium*. At the mouth of the cell the cuticle becomes suddenly exceedingly thin, so that the anterior portion of the body is quite mobile, and by means of special retractor muscles (*m*) may be withdrawn within the zoœcium. The retraction is a process of invagination, similar to what occurs in the withdrawal of the pharynx of the Annelida, the most anterior lophophoric part of the retracted portion not, however, sharing in the invagination: the whole process indeed is similar to what may be obtained when one finger of a glove is caught from within somewhat less than half way from the tip and drawn down towards the palm ; half of the lower portion will thus be invaginated within the other half, while the tip of the finger remains uninvaginated.

The portion of the body-wall enclosed by the ectocyst is thin, its longitudinal muscles being for the most part separated in the form of bands traversing the cœlom and functioning as retractors, while the circular muscles are specially developed as a rule only around the mouth of the cup, which may by their action be closed over the retracted tentacles. A relatively spacious cœlom, containing a colorless corpusculated hæmolymph is present, and is lined by flattened peritoneal cells, some of which bear tufts of cilia. The intestine has a characteristic Y-shape (Fig. 116), its posterior portion being prolonged backwards to form a cæcal pouch, from the extremity of which a band or plate, the *funiculus* (Fig. 116, *f*), containing in some cases muscular fibres, and lined by peritoneal cells, arises, and passes backwards to be inserted into the ectocyst posteriorly. The anus (*a*), as already stated, opens on the anterior surface of the body, outside the limits of the lophophore, and between it and the mouth lies the nerve-ganglion, which is frequently hollow and sends off nerves to the various portions of the body

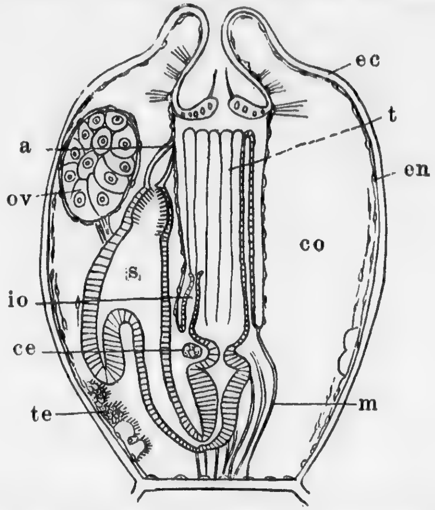


FIG. 115.—DIAGRAM OF THE STRUCTURE OF *Alcyonidium albidum* (after PROUHO).

a = anus.
ce = ganglion.
co = cœlom.
ec = ectocyst.
en = endocyst.
io = intertentacular organ.
m = retractor muscle.
ov = ovary
t = tentacles.
te = testis.

As in the Endoprocta, a heart and a blood vascular system is entirely wanting. Special excretory organs seem to be wanting in the marine Ectoprocta, excretion being performed apparently by the hæmolymph-corpuscles and other mesoderm-cells, especially those of the funiculus, as well as by the granular cells of the stomach and cæcal pouch. In *Cristatella*, a fresh-water form, however, a pair of ciliated canals opening into the cœlom by ciliated funnels have been described, and presumably are excretory in function, the two canals uniting together to open to the exterior by a single pore situated between the mouth and anus. Up to the present, however, these structures have not been observed in other forms and apparently they do not exist in the marine forms.

In some of these latter (*Alcyonidium*, etc.), however, a ciliated tubular structure, which communicates at one end with the cœlom and opens to the exterior between the tentacles at the other, occurs and has been termed the *intertentacular organ* (Fig. 115, *io*). It suggests a nephridium in its relations, but apparently does not possess an excretory function, but serves as an exit for the reproductive elements to the exterior. In other marine forms and in all the fresh-water genera such special reproductive ducts have not been observed, and the mode of escape of the sexual products in these forms is still unknown. Many of the Ectoprocta are hermaphrodite, the ova and spermatozoa (Fig. 115, *ov*, *te*) arising from the peritoneal mesoderm, frequently from that surrounding the funiculus. Whether, however, hermaphroditism is a characteristic of the order or not is a point as yet undecided.

1. Suborder *Phylactolæmata.*

The members of this suborder are exclusively inhabitants of fresh water and are characterized by the tentacles being arranged in a horseshoe-shaped manner (except in the genus *Fredericella*, where they form a circle), and by the occurrence of a well-developed lobe or *epistome* overlapping the mouth.

The colonies assume various shapes in different genera, being sometimes dendritic and incrusting stones or other bodies, as in *Fredericella*, or forming compact masses, as in *Alcyonella* and *Lophopus*, or even being capable of motion, as in *Cristatella*. In some forms, e.g. *Lophopus*, the ectocyst possesses a gelatinous consistency, though usually it is chitinous, and the various zoœcia are in free communication with one another, not being separated by transverse partitions.

In addition to multiplying by the usual processes of budding and by ova, the Phylactolæmata develop upon the funiculus special internal buds, termed *statoblasts*, which are enclosed within dense chitinous capsules. These are set free by the dying and disintegration of the parent and, being protected by the resistant capsule, retain their vitality under conditions, such as cold and dryness, that destroy the adult individual. They are evidently a special provision for the perpetuation of the species developed in accordance with the fresh-water habitat, in which the organisms are exposed to various conditions not apt to be met with in the ocean; it is interesting to note in this connection the occurrence of gemmules in the fresh-water sponges which are strictly comparable to the statoblasts and have a similar significance.

2. Suborder *Gymnolæmata*.

The Gymnolæmata are distinguished from the Phylactolæmata by being, with the single exception of the genus *Paludicella*, marine in habitat, by the tentacles being arranged in the form of a circle, and by the invariable absence of an epistome.

As in the Phylactolæmata, the colonies vary greatly in form, being in some cases encrusting, *Membranipora*, *Flustra*, in others branching, *Scrupocellaria*, or in others again massive, *Alcyonidium*; and furthermore the ectocyst presents varying degrees of consistency, being frequently chitinous, but occasionally somewhat gelatinous or calcified to a greater or less extent. The zoœcia are not in free communication with each other, but each is closed below or posteriorly by a transverse chitinous plate in which perforations are said to be present, though doubt has recently been thrown upon their existence as perforations. In shape, too, the zoœcia like the colonies vary greatly, especially so far as their mouths are concerned, and it is possible to divide the Gymnolæmata into three groups or tribes, based upon these differences. In the tribe *Cyclostomata* the zoœcia are usually cylindrical, and the mouth is circular and destitute of any appendages; in the *Ctenostomata* the mouth is closed during retraction by a series of bristles which surround it (*Alcyonidium*); while in the *Chilostomata*, in which the ectocyst is usually firm and frequently calcified, the mouth is closed by a lid, the *operculum*, furnished with special muscles (*Bugula*, *Membranipora*).

In this last-named tribe a polymorphism of the individuals composing a colony is frequently found. Scattered among the ordinary individuals others, the *Avicularia* (Fig. 116, *av*), may be found having the appearance of a bird's head, the lower beak being fastened to the head by a hinge and having inserted into it strong muscles; bunches of sensory hairs are also present, and when these are stimulated the lower beak is rapidly snapped against the upper and the stimulating organism thus caught. There can be little doubt but that these Avicularia are specially modified individuals whose head and upper beak represent the ordinary individual, while the lower beak may possibly be the equivalent of the operculum; physiologically they have been usually regarded as specialized for the purpose of catching food for the ordinary individuals, but it is not improbable that their services may rather be of a cleansing nature, removing from the colony particles of dirt and the excreta, which by accumulating might interfere with the proper function of the tentacles. Another polymor-

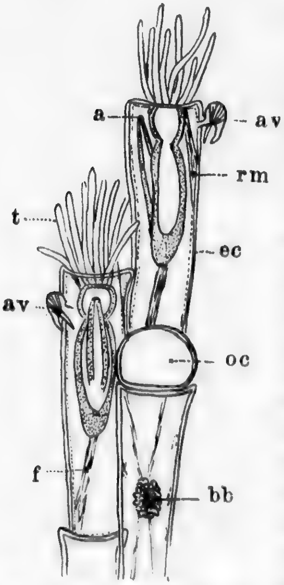


Fig. 116.—Portion of a Colony of *Bugula*.

a = anus.
av = avicularia.
bb = brown body.
ec = ectocyst.
f = funiculus.
oc = ovicell.
rm = retractor muscle.
t = tentacles.

phic form is known as the *Vibracula*, and consists of a slender filament movably articulated to a rounded structure corresponding to the head of the Avicularia; the filaments wave continually to and fro and are probably tactile in function. In many forms, too, in the neighborhood of the mouths of the ordinary individuals sac-like pouches occur, in which the ova undergo their development. These structures, known as *ovicells* (Fig. 116, *oc*), or *oœcia*, have also been considered modified individuals, but seem rather to be organs of the ordinary individuals, arising as a pouching of their walls. Finally, not infrequently certain individuals relinquish their nutritive function and serve as root-like anchors or stem-like supports for the entire colony.

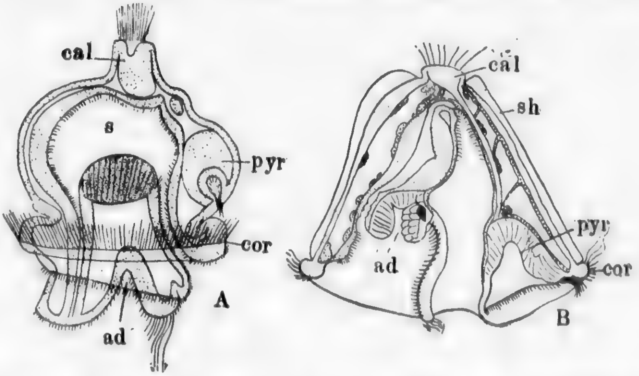


FIG. 117.—*A*, LARVA OF *Pedicellina* (after HATSCHEK); *B*, *Cyphonautes* (after PROUHO).

ad = adhesive organ.
cal = calotte.
cor = corona.
s = stomach.
sh = shell.
pyr = pyriform organ.

As regards the internal structure of the Gymnolæmata it is unnecessary to add anything to what has already been stated in describing the general characteristics of the order Ectoprocta.

Development of the Polyzoa.—The larva of *Pedicellina* (Fig. 117, *A*), which may be taken as a type of the Endoprocta, is a somewhat dome-shaped organism, the summit of the dome being occupied by an apical thickening (*cal*) bearing a tuft of cilia, while at the margin there is a stout ciliary band, the corona (*cor*). The cavity of the dome is occupied by the U-shaped digestive tract (*s*), the mouth and anus both opening within the circle formed by the corona, a deep depression, the vestibule, lying between the two. In the cœlom above the floor of the vestibular depression are a number of mesoderm-cells, and also a ciliated canal composed of a single row of perforated cells and probably excretory in function. Upon one surface of the larva between the marginal ciliated band and the apical thickening is a peculiar glandular organ termed the cement-gland (*pyr*), around the mouth of which are situated a number of strong cilia.

The development of this larva into the adult form is accompanied by a number of remarkable changes, which in their details and significance are not yet thoroughly understood. The larva settles upon the ventral or oral face and shortly thereafter one wall of the vestibule becomes pushed over towards the other and eventually unites with it, the original vestibular cavity becoming divided into two portions, one of which remains in connection with the surface of fixation and later degenerates, while the other has opening into it the mouth and anus, though the former opening at about this period becomes closed. Later a remarkable rotation through 180° of the digestive tract, together with the portion of the vestibule in connection with it, occurs, the portion of the body immediately above the point of fixation elongating to form the stalk of the adult, becoming at the same time filled with mesodermal tissue. The mouth opens again into the vestibular cavity, the tentacles arise from the wall of the cavity which later opens to the exterior, the adult form being thus assumed. The fate of the apical thickening and of the cement-gland is uncertain; they have been described as degenerating without taking any part in the formation of the adult organs, though it has been suggested that the apical thickening may give rise to the nervous system of the adult.

The form of the larvæ in the Ectoprocta is subject to considerable modification. In *Membranipora* and some other genera the larva is known as the *Cyphonautes* (Fig. 117, *B*), having been so designated before its life-history was elucidated. It has a somewhat triangular outline and is characterized by being enclosed in a bivalved chitinous shell (*sh*). At the apex of the triangle is the apical thickening (*cal*), with its elongated cilia, while around the base there is to be found the corona (*cor*). A well-developed digestive tract is present, both the mouth and anus opening upon the basal surface of the triangle, and therefore within the area enclosed by the corona.

This vestibule is a deep depression of the oral surface of the larva, differing from that of the *Pedicellina* larva only in having an arch-like thickening of its walls (only one side of the arch is represented in the figure) which imperfectly separates an oral portion of the vestibule from a posterior or anal portion, a glandular depression situated in the roof of this latter portion constituting the adhesive organ (*ad*). In front of the oral vestibule is situated a ciliated depression from which projects a tuft of long cilia and which appears to correspond to the cement-gland of the *Pedicellina* larva and to a glandular structure in the more modified Ectoprocta larvæ, known as the pyriform organ (*pyr*), by which name it may be known here. The similarity of this larva to that of *Pedicellina* is clear, the details of organization of the two forms agreeing part for part; in other Ectoprocta, however, great differences are to be found. In the genus *Bugula*, for example, the larva (Fig. 118) is a barrel-shaped organism at the one extremity of which is a thickening, the calotte (*cal*), which appears to correspond, in part at any rate, to the apical thickening or dorsal organ, as it is sometimes termed, of *Pedicellina* and *Cyphonautes*. The sides of the barrel are formed by a circle of elongated cells forming the corona and equivalent to the marginal corona of the other larvæ; it does not, however, form a simple band in *Bugula*, but its cells are much shorter on one of the faces of the embryo than elsewhere, producing a well-marked groove at the apex of which lies the pyriform organ (*pyr*) whose homologies in *Cyphonautes* have already been pointed out. A peculiarity of this larva is the entire absence of a digestive tract, the lower end of the barrel being occupied by a depression, the adhesive organ (*ad*).

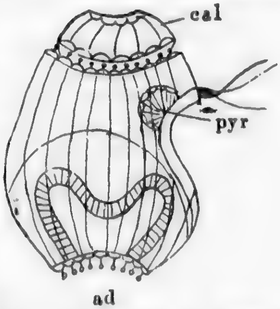


FIG. 118.—LARVA OF *Bugula flabellata* (after BARROIS). Letters as in Fig. 117.

Between such a larva as that just described, entirely destitute of a digestive tract, and that of *Cyphonautes* intermediate stages occur, as for instance in the larvæ of the Cyclostomata, in which the digestive tract is represented by a yolk-laden mass of tissue, having little resemblance, however, to the differentiated endodermal tube of *Pedicellina*. The occurrence of such forms, however, shows that the absence of the tract in *Bugula*, etc., is the result of progressive degeneration, such larvæ as those of *Pedicellina* and *Cyphonautes* representing the primitive condition more nearly than the remarkable larva of *Bugula*.

The transformation of the Ectoproctous larvæ into the adult is even more remarkable than that of *Pedicellina*. Fixation takes place by the oral surface, the adhesive organ being evaginated for the purpose, and is succeeded by a degeneration of the corona and pyriform body. In *Cyphonautes* the digestive system completely degenerates likewise, a new one being formed later, the tissue in the neighborhood of the apical thickening taking a prominent part in its formation. In those larvæ which are destitute of a digestive tract one, corresponding to the second one of *Cyphonautes*, develops after fixation, likewise from the tissue of the apical thickening. The exact method of this regeneration, for so it may be considered, can hardly be described here without leading to a recapitulation of details too minute for the scope of this work. It may be remarked, however, that the phenomena do not seem to merit the designation of an alternation of generations, as might at first sight be supposed, but are rather simply a metamorphosis the significance of which is at present decidedly obscure.

Budding of the Polyzoa.—As already stated, colony formation by budding is a characteristic feature of the Polyzoa, *Loxosoma* alone not presenting this method of growth, though like other forms it reproduces by budding, the buds, however, separating at an early stage from the parent. In the Endoprocta a stolon arises from near the point of fixation of the primary individual which develops from the ovum, mesoderm tissue from the stalk of this individual migrating into the stolon, but there is no prolongation into it of the parental endoderm. At a more or less definite part of the stolon the ectodermal cells thicken and later on invaginate towards the centre of the stolon. This invagination becomes surrounded by mesoderm already present in the stolon, and later differentiates into two cavities, one of which retains connection with the exterior and forms the vestibular chamber, from the walls of which the tentacles develop, while the other becomes the digestive tract, its original connection with the vestibular cavity becoming the anus, the mouth developing later as a depression of the floor of the vestibular cavity which joins the stomach. It is interesting to note that from the ectodermal invagination the nervous system as well as the digestive tract develops.

In the Ectoprocta practically the same method obtains in the budding, though the stolon is represented by the tip of a branch or even by the tissue in the neighborhood of the mouth of the zoœcium. The colony resulting from continued budding becomes accordingly as a rule much more compact than in the Endoprocta, each polypide being more or less approximated to its predecessor.

Closely related to the process of budding is that of regeneration, also of frequent occurrence among the Polyzoa. Among the Endoprocta *Pedicellina* shows the process in a periodical though not simultaneous moulting of the polypides, new ones developing from the tip of the stalk which bore the amputated polypide. Here, as in ordinary budding, the tissues concerned appear to be ectoderm and mesoderm, the stalk containing no prolongation of the original endoderm.

In the Ectoprocta, however, regeneration is carried to a greater extent. In examining any colony of *Bugula*, for example, in some of the zoœcia in addition to the polypide a brown mass may be seen, the so-called "brown body" (Fig. 116, *bb*); in others the brown body may be seen without any distinct polypide. This body is the result of the degeneration of the digestive tract and other organs of the original polypide, only its body-wall or endocyst persisting, from which new organs are developed and the polypide regenerated. The significance of this process is not clear, but it has been suggested that it stands in relation to the process of excretion, the formation of the brown body occurring in forms which do not possess any special excretory organs. It is now known that in the marine Ectoprocta the excretory products are taken up in part by the cells of the stomach and cæcal pouch, a fact which seems to harmonize with the suggested significance of the brown body.

The formation of a new polypide from ectoderm and mesoderm apparently is a difficult fact to explain on the theory of the germ-layers. It is possible, however, to regard the tissue from which buds arise as undifferentiated embryonic tissue passed on from polypide to polypide and traceable back to the embryonic tissue of the ovum. In the formation of each polypide a certain amount of the tissue becomes differentiated, but some still retains its embryonic character, a continuation of the budding process being thus possible.

Affinities of the Polyzoa.—There seems to be little room for doubt but that the Endoprocta represent more nearly the original Polyzoa than do the Ectoprocta. Their colony formation is of a more simple form than that of the other group, they possess nephridia which are wanting in the majority of the Ectoprocta, and their development is much simpler, the highly modified larva of the marine Ectoprocta having undoubtedly been derived from one approximating in structure that of *Pedicellina*, *Cyphonautes* representing a stage in the evolution.

Similarities have been traced between the *Pedicellina* larva and the Annelid Trochophore, and it is not improbable that this may have been the true derivation of the group, in which case the Polyzoa are to be regarded as forms which have never possessed any traces of metamerism, but stand in about the same relationship to the Annelida as do the Rotifera.

Another view, however, which has had ardent supporters is that which recognizes a relationship between the Polyzoa and *Phoronis*. There is a lophophore in both, likewise a U-like bending of the digestive tract, and the nephridia of *Phoronis* may be considered comparable to those of the Endoprocta. But here the similarity ceases. The anus in *Phoronis* is outside the limits of the lophophore and is comparable in position with that of the Ectoprocta, a point which tells against this phylogeny since these forms have been shown to be less primitive than the Endoprocta. If, however, this phylogeny should prove to be correct, it will show a descent for the Polyzoa from metameric Annelids, through the Gephyrea, since it is to this group that *Phoronis* seems to be most nearly related.

II. CLASS **BRACHIOPODA**.

The *Brachiopoda* constitute a very well-defined group whose present poverty in species is in striking contrast to its great development during Palæozoic times. Like the Polyzoa they possess a tentaculate lophophore (Fig. 120, *lp*) which usually takes the form of two exceedingly elongated, sometimes spirally-coiled, arm-like processes projecting, one on either side, from the anterior portion of the body, and furnished upon their outer or posterior border with tentacles. The body is usually somewhat short and stout, and prolonged posteriorly into a peduncle (*pe*) or stalk which is in some cases at least provided with adhesive papillæ and serves as an anchor.

The most characteristic feature of the Brachiopoda is, however, the presence of a bivalved shell (Fig. 119) similar to that of a bivalve Mollusk, with which forms the Brachiopods were until comparatively recently associated. From near the base of the peduncle, upon the dorsal and ventral surfaces of the body, a fold of the body-wall is found, which contains a cavity in communication with and indeed in reality a portion of the cœlomic cavity. These two folds are of sufficient size to enwrap or enclose the body and the lophophore and are termed the *mantle-lobes* (Fig. 120, *m*), the space between them and the body being known as the *mantle-cavity*. They subserve largely if not entirely the function of respiration, the portion of the cœlom which they contain being more or less divided up into a system of lacunæ through which the hæmolymph circulates. Upon the outer surface of each mantle-lobe, and formed by it, is a valve of the shell, composed of a certain amount of organic matter, but largely of carbonate of lime. Since the mantle-lobes are dorsal and ventral in position, so too are the valves of the shell, and consequently their hinge-line is posterior and their mouth anterior. In a number of forms, which may be grouped together as the suborder *Testicardines*, the shells along the hinge-line are provided with interlocking teeth, a true hinge being present, the peduncle in these cases perforating a backward prolongation or beak of the lower valve. In a few genera, however, forming the suborder *Ecardines*, no such hinge is present, the peduncle passing out between the two valves of the shell. Special muscles are present extending from one valve of the shell to the other and are necessary both for the opening and the closing of the shell, and furthermore it should be noted that except for a slight difference in concavity both valves of the shell are similar and symmetrical.

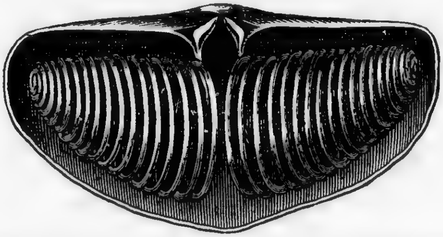


FIG. 119.—DORSAL VALVE OF *Spirifer*, SHOWING ARM SKELETON (after LEUNIS).

It will be seen by comparing the various facts mentioned here with what is said on p. 327 regarding the shell of the bivalve Mollusks that the structures in the two groups are very different. This difference is emphasized by the presence, in the majority of the Testicardines, of a calcareous support for the coiled lophophore attached to the inner surface of the dorsal valve (Fig. 119). It consists of a pair of calcareous rods which project downwards and forwards, uniting to form a transverse arch, and may give rise on each side to a spirally-wound process upon which the coils of the lophophore rest.

The body-wall is composed of an outer layer of ectoderm from which numerous papillæ or in some cases branching processes arise, projecting into corresponding cavities or tubes in the substance of the shell-valves. Below the ectoderm is a more or less homogeneous connective tissue containing cells and recalling the mesoglœa tissue of the Cœlenterates. Scattered muscle-fibres, arranged transversely and longitudinally, occur in the mantle-lobes and in the body-wall, but there are no definite muscular layers such as are found in the Annelida, though the longitudinal muscles of the peduncle are well developed. Special muscles, which cannot be considered differentiations of the musculature of the body-wall, traverse the cœlom from one valve of the shell to the other, one pair, the divaricators, being inserted in such a way as to cause by their contraction a separation of the two valves, while another pair, the adductors (Fig. 120, *am*), approximate them. Other muscles also occur, such as the adjustores, which produce lateral movements of the shell-valves, and protractors and retractors (Fig. 120, *rm*) of the peduncle.

The cœlom is lined by a peritoneal epithelium and contains a corpusculated hæmolymph which is driven about through the cœlomic spaces, and the lacunæ in the mantle-folds and the lophophore which communicate with them, by the contractions of the body-wall and the musculature, there being no distinct heart or blood-vessels. A dorso-ventral mesentery which slings the intestine is present and divides the body-cœlom more or less completely into two lateral chambers, and furthermore two transverse partitions or dissepiments occur in several forms and divide the cœlom into anterior, middle, and posterior compartments, an arrangement recalling the metamerism of such a form as *Sagitta* (p. 137).

The mouth opens at the anterior end of the body between the two lophophoric arms and leads into a short, somewhat muscular œsophagus, which posteriorly communicates with a stomach-like dilatation (Fig. 120, *i*) into which open the ducts of one or more pairs of branching tubular glands—the so-called liver or digestive glands (*l*). Behind the stomach lies the intestine, which, in most of the Ecardines, such as *Lingula*, bends upon itself and opens into the mantle-cavity in the mid dorsal line near the anterior end of the body. In *Crania*, however, it opens posteriorly, while in *Terebratulina, Argiope,* and *Waldheimia,* in fact in all the Testicardines, it ends blindly, the anus being wanting.

The nervous system consists of an œsophageal ring lying in the connective tissue substance, the lower portion being in connection with the ectoderm and slightly swollen, representing probably the subœsophageal ganglion of the Annelida; a similar swelling in the dorsal portion of the ring represents the supraœsophageal ganglion, and in addition there are usually two further lateral ganglion-like swellings. Nerves pass off from the upper ganglion to the lophophore and other regions, and from the lower one to the mantle, muscles, etc., both sets terminating in the superficial layers of the lophophore-tentacles or of the mantle in a network of ganglion cells and fibres. No trace of a ventral nerve-cord in addition to the subœsophageal ganglion is present.

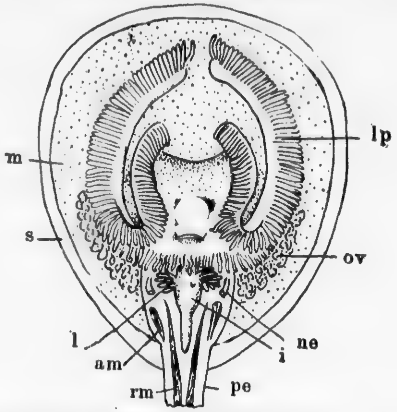
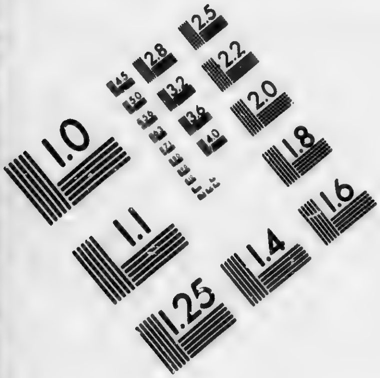


FIG. 120.—STRUCTURE OF *Terebratulina septentrionalis.*

am = adductor muscle.
i = intestine.
l = liver-lobes.
lp = lophophore.
m = mantle.
ne = nephridium.
ov = ovary.
pe = peduncle.
rm = retractor muscle.
s = shell.

Sense-organs are but poorly developed, neither eyes nor auditory organs occurring. The tentacles on the lophophoric arms are in all probability sensory, as indicated by their rich nerve-supply, and the papillæ of the mantle-ectoderm which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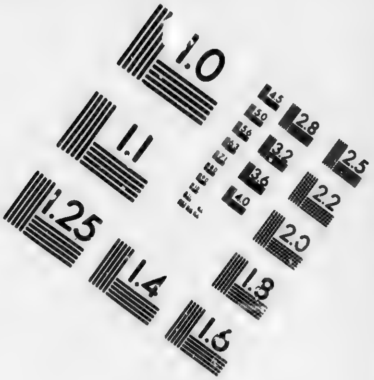
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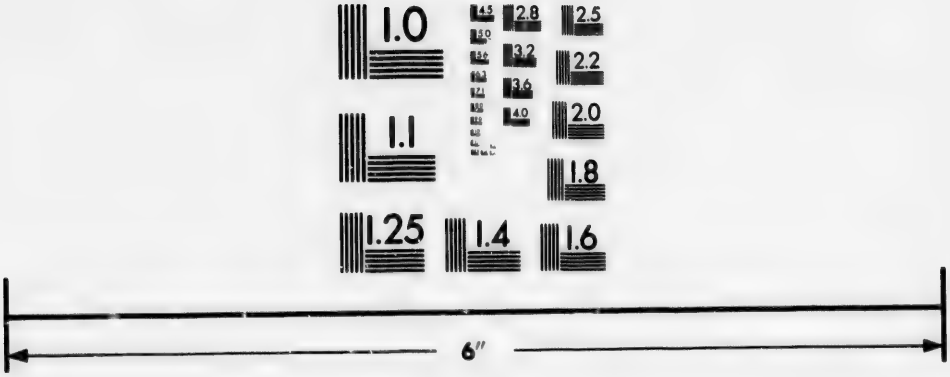
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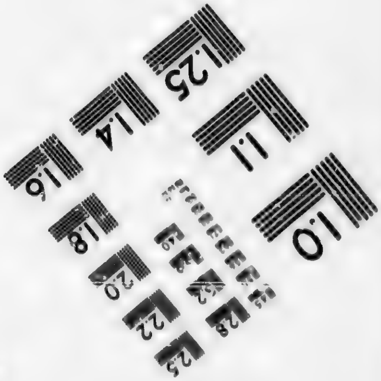
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project into the canals of the shell have been stated to be sensory, containing an axial nerve-fibre terminating in a sensory cell.

The nephridia (Fig. 120, *ne*) are represented by two or four (*Rhynchonella*) funnel-shaped short tubes which open by a fimbriated mouth at one extremity into the cœlomic cavity and, rapidly narrowing towards the outer end, open by a small pore into the mantle-cavity. In addition to their probable excretory function, these structures, as in some of the Annelida, serve also as ducts for the passage to the exterior of the reproductive elements. These are derived from the cœlomic peritoneum and form branching masses (Fig. 120, *ov*) lying in some cases in the cœlomic spaces of the mantle, or in addition extending into the body, as in most Ecardines, or, as in *Terebratulina*, confined to this region. Most of the Brachiopods are bisexual apparently, though it is possible that *Lingula* and perhaps some other forms may be hermaphroditic, the male and female elements maturing at different times.

Development and Affinities of the Brachiopods.—The Testicardines are characterized by the occurrence of a free larval stage destitute of a shell. In *Argiope* (Fig. 121) it is apparently divided into four segments, the most anterior of which bears two eye-spots and assumes an umbrella-like form, long cilia projecting from the margin. The third segment develops two folds which enclose the posterior segment and bear on their margin bunches of setæ inserted in seta-sacs and recalling the setæ of certain Annelid larvæ. After swimming about for a time the larva settles down and fastens itself by the posterior segment and the mantle-lobes turn forward to enclose the anterior segments. The posterior segment becomes the peduncle of the adult, and the shell develops on the surface of the mantle-lobes, whose bunches of setæ are thrown off. The mouth makes its appearance only after fixation just ventral to the eye-spots, and around it there develops a ring of tentacles placed somewhat obliquely, and

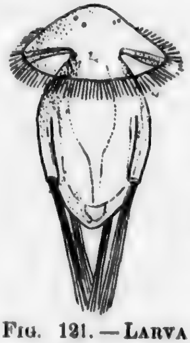

FIG. 121.—LARVA OF *Argiope* (after KOWALEWSKI).

later elongating laterally to form the coiled lophophore with its numerous tentacles.

The early stages of the development of the Ecardines is not known, but in *Lingula* the larva is free-swimming long after the shell has formed, the peduncle being late in developing. In this form also the lophophore arises as a circle of tentacles surrounding the mouth and subsequently elongates laterally.

The affinities of the Brachiopods have long been an open question. They were by early writers regarded as Mollusca, later as Annelida or closely related to that group, but are now usually considered to be more nearly related to the Polyzoa than to any other forms and to be most properly associated with them, the general likeness of a young *Lingula*, for instance, to a Polyzoan being very striking. The presence of the mantle-lobes and the shell seem to mark the Brachiopoda as something far removed from the other members of the type Prosopygia, but it must be remembered that in the larval Ectoproctous Polyzoa the corona behaves in a manner closely similar to the Brachiopod mantle and it is not impossible that the two structures may have something in common.

Another distinguishing feature of the Brachiopods is the indication of a segmentation. The presence of two dissepiments and in *Rhynchonella* of two pairs of nephridia certainly suggests metamerism, but objection has been raised to the dissepiments having any metameric significance, on the ground that they do not bear the proper relationships to the body axis to be regarded as comparable to the dissepiments of the Annelida. It has been stated by some authors as a characteristic of the Prosopygia that their body axis is bent upon itself so that the two ends are approximated and one surface, the dorsal, is almost obliterated, while the other, the ventral, is very much enlarged, as seems to be actually the case in *Phoronis*. It must be remembered, however, that the terms dorsal and ventral are not to be defined by reference to the digestive tract alone, but other structures have also to be taken into consideration. Thus it is quite possible that in the Polyzoa the approximation of the mouth and anus indicates simply a bending of the digestive tract and a migration forwards of the anus and not necessarily a bending of the body axis; and the varying position of the anus in the Ecardinate Brachiopods tends to support this idea, the body axis in *Crania* with a terminal anus certainly being similar to that of *Lingula*, in which the anus lies far forwards. In this connection, too, the arrangement in *Sipunculus* is of interest, the nerve-cord showing the usual relations to the body axis, while the digestive tract is bent upon itself and the anus opens far in front of the posterior extremity. In the Sipunculacea there can be no question of a difference of the body axis in the various forms, and it seems probable that the supposed bending of the body axis in the Prosopygia has not really occurred, but that there has been simply a bending of the digestive tract and a migration forwards of the anus.

If this be the correct way of regarding the matter, then there is no reason for disputing the homology of the dissepiments of the Brachiopoda with those of the Annelida, and the idea that they represent a metamerism is borne out by the arrangement of the two pairs of nephridia of *Rhynchonella*. The question is then, Does the metamerism of the Brachiopods indicate a descent of the Prosopygia from metameric ancestors, i.e., from Annelids through Gephyrean-like forms, or is it a structural feature independently acquired by the Brachiopods? The evidence at our disposal is not sufficient for the solution of this problem, and all that can be maintained is that a very close relationship exists between the Polyzoa and the Brachiopoda.

SUBKINGDOM METAZOA.

TYPE PROSOPYGIA.

I. Class POLYZOA.—Small, usually colonial forms; lophophore circular or horseshoe-shaped; no bivalve shell; no mantle-lobes.

  1. Order *Endoprocta.*—Mouth and anus both within the area enclosed by the lophophore. *Loxosoma, Pedicellina, Ascopodaria, Urnatella.*

  2. Order *Ectoprocta.*—Anus outside the area enclosed by the lophophore.

    1. Suborder *Phylactolæmata.*—Fresh-water forms; lophophore usually horseshoe-shaped; epistome present. *Fredericella, Alcyonella, Lophopus, Cristatella.*

    2. Suborder *Gymnolæmata.*—Usually marine; lophophore circular; no epistome.

      Mouth of zoœcium without bristles or operculum (*Cyclostomata*). *Crisia.*

      Mouth of zoœcium usually surrounded by bristles which close over it (*Ctenostomata*). *Paludicella, Alcyonidium.*

      Mouth of zoœcium provided with an operculum (*Chilostomata*). *Membranipora, Bugula, Flustra, Scrupocellaria.*

II. Class BRACHIOPODA.—Non-colonial and of moderate size; lophophore usually arm-like and coiled into a spiral; mantle-lobes and bivalve shell present.

  1. Order *Ecardines.* — Shell-valves not hinged; peduncle protrudes between the valves; anus present. *Lingula, Crania.*

  2. Order *Testicardines.*—Shell-valves hinged; peduncle when present protruding through perforation in the ventral shell; anus wanting. *Terebratula, Waldheimia, Argiope, Rhynchonella.*

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CHAPTER XII.

TYPE MOLLUSCA.

WHILE the Annelida are characterized by an elongated form of body, the Mollusca present the opposite condition, being compact, non-metameric organisms, though at the same time primitively bilateral in the arrangement of their organs. Upon the external surface of the body a cuticular secretion is formed in which usually particles of carbonate of lime are deposited, a calcareous shell being thus developed, which encloses more or less perfectly the soft body, assuming, however, very different forms in the various groups. It is essentially a dorsal structure developed in the majority of forms from a depression on the dorsal surface of the body—the shell-gland (Fig. 122, *f*)—and in some forms may be entirely confined to this area. Usually, however, a circular or bilateral fold of the body, the mantle (*c*), arises peripheral to the margins of the shell-gland and extends downwards towards the ventral surface, and the growth of the shell may accompany that of the mantle-fold, so that the entire body is enclosed by or may be retracted within the greatly-developed shell. Even in cases, however, in which the shell is but slightly developed the mantle-folds retain their development, forming a marked structural feature of the Mollusca, and enclosing a more or less spacious cavity, the mantle-cavity, in which lie the respiratory organs and into which the intestine and nephridia and reproductive ducts open.

The body-wall is formed of an external layer of ectoderm, below which a more or less thick layer of muscle-tissue is found whose fibres sometimes show the arrangement in circular and longitudinal layers characteristic of the Annelida, but usually the simplicity of this arrangement is interfered with by a development of connective tissue in which irregularly-arranged muscle-bundles lie. Upon the ventral surface of the body there is a special thickening of the muscle-tissue to form a "foot" (Fig. 122, *p*), which assumes a great variety of forms, and special muscles are developed for its protraction or retraction when this is necessary, as well as for the closure of the shell in those forms (Pelecypoda) in which it is a bilateral structure.

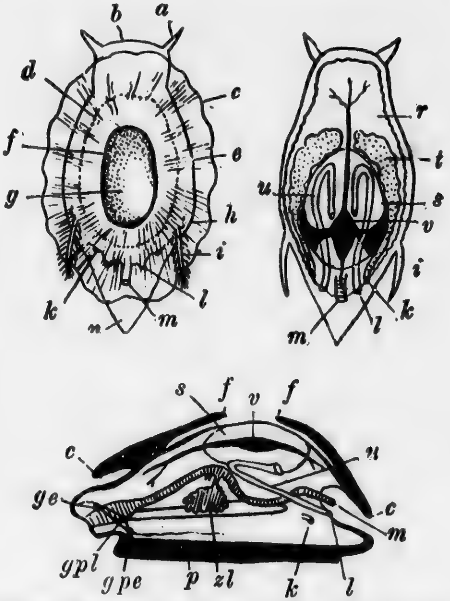

FIG. 122.—DIAGRAMS SHOWING THE ARRANGEMENT OF THE ORGANS IN AN IDEAL MOLLUSK (after LANKESTER).

a = tentacle.
b = head.
c = margin of mantle
d = margin of shell.
e = edge of body.
f = edge of shell depression.
g = shell.
gc = cerebral ganglion.
gpe = pedal ganglion.
gpl = pleural ganglion.
h = osphradium.
i = ctenidium.
k = reproductive pore.
l = nephridial pore.
m = anus.
n and *p* = foot.
r = cœlom.
s = pericardium.
t = testis.
u = nephridium.
v = ventricle of heart.
zl = liver.

The cœlom is in some forms a relatively spacious cavity, traversed, however, even in these cases by thin bands of connective tissue, but more usually it is reduced to a system of lacunar spaces (a so-called schizocœl) by the development of muscle-bundles traversing it in various directions. A special portion of it (the so-called enterocœl) is, however, always enclosed in definite walls lined by a peritoneal layer of cells, forming a cavity, the pericardium (Fig. 122, *s*), which lies normally near the dorsal surface of the body, containing the heart and having the inner ends of the nephridia (*u*) opening into it. The blood vascular system consists of a primitively three-chambered heart (Fig. 122, *v*) enclosed within the pericardium and composed of a tubular muscular ventricle and two wing-like auricles which open into the ventricle, their openings being guarded by valves which prevent regurgitation. From the anterior and posterior extremities of the ventricle aortæ arise, which, however, as a rule soon lose themselves in the cœlomic lacunæ. There is thus no distinction between the blood and pseud-hæmal fluids in the Mollusca, since the blood vascular system is not closed. The blood is a colorless fluid in which numerous amœboid cells float and which holds in solution a substance, hæmocyanin, which subserves a respiratory function in a manner similar to the hæmoglobin of the Vertebrata.

The heart is a systemic heart, as is usual in the Invertebrata, and contains only aerated blood, which it propels through the lacunæ of the body. Returning from these, the blood passes either directly to the respiratory organs or branchiæ, or else a greater or less portion of it traverses first the walls of the nephridia and then passes to the branchiæ. From these, in which it is aerated, it is received into the auricles, and on their contraction is forced into the ventricle.

In some Mollusca respiration is carried on by the general surface of the body, but such an arrangement must be regarded as the exception. As a rule special respiratory organs are present in the form of one or more pairs of plume-like processes (*ctenidia*) of the body-wall (Fig. 122, *i*) lying free in the mantle-cavity. They have various forms in the different groups, but consist essentially of a central axis containing an afferent and efferent canal for the blood and bearing a single or double series of filaments whose walls are thin and whose ectoderm is ciliated, an interchange of the gases of the blood with those of the water contained in the mantle-cavity being thus readily effected, a renewal of the water constantly taking place in consequence of the action of the ectodermal cilia. The thin-walled mantle-fold is, however, a very efficient adjunct to the branchiæ in respiration, the spaces within the fold being portions of the lacunar cœlom and consequently containing blood; indeed in some cases the mantle assumes completely the respiratory function, the ctenidia becoming rudimentary.

The digestive tract is a usually more or less coiled or convoluted tube in which various regions may be distinguished. In a few forms, characterized either by the slight development of the mantle or its development as two lateral folds, the anus is terminal in position, but when an extensive circular mantle-fold is developed the intestine bends upon itself and opens upon the side of the body, more or less anteriorly, into the mantle-cavity. Immediately behind the mouth chitinous teeth (Fig. 123, *hj*) are usually developed in the wall of the pharynx, and behind these a large muscular thickening generally occurs, the buccal mass, in connection with which is developed a characteristic Molluscan structure, the lingual ribbon or *radula* (*rd*). The sides and floor of the pharynx in this region are largely thickened by the development in them of muscular tissue (*im*). The thickening of the floor is usually so extensive as to project into the pharyngeal cavity, forming

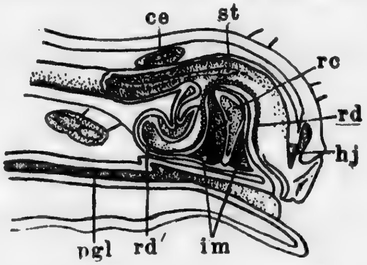

FIG. 123.—BUCCAL MASS AND RADULA OF *Helix* (after HOWES).

ce = cerebral ganglion.
hj = horny jaw.
im = intrinsic muscles.
pgl = pedal gland.
rc = radular cartilage.
rd = radula.
rd′ = radular sac.
st = opening of salivary gland.

the so-called tongue, and in addition to the muscular tissue two or more pieces of cartilage, the radular cartilages (*rc*), are frequently found in it. Covering the tongue is a stout chitinous membrane, the basal membrane, which bears upon its surface a usually enormous number of chitinous teeth arranged in transverse rows, so that the basal membrane and the teeth, together constituting the radula (*rd*), recall somewhat the appearance of a flat file. Behind the tongue the floor of the pharynx is produced downwards and backwards into a pouch, the *radula-sac* (*rd'*), sometimes of considerable length, into which the radula is continued on the ventral wall, the cells (*odontoblasts*) which form the teeth as a cuticular secretion, lying at the bottom of the sac. The tongue, with its radula, can be protruded to a greater or less extent from the mouth by special protractor muscles, and its intrinsic muscles serve to give it a slow licking movement, whereby the radula acts as in the manner of a file or rasp upon the object with which it is in contact. Owing to this action the radula is continually being worn away at its anterior end, but is also continually being pushed forward upon the tongue by the addition of new teeth to its posterior portion at the base of the radula-sac.

In connection with the digestive tract various glands are usually present, of which the most constant are the salivary glands and the "digestive glands." The former open into the pharynx and in some cases reach extensive devolopment; their function for the most part is but little understood, but in some predaceous Gasteropods their secretion has been found to contain a considerable amount of free sulphuric acid which probably serves to soften the calcareous shell of Echinoderms and other Mollusca which serve these forms as food. The "digestive glands" open into a dilated portion of the intestine, usually termed the stomach, and are usually paired, voluminous, much-branched tubular glands whose function is indicated by the name applied to them. They seem to be the physiological representatives of the pancreas of the Vertebrata, and to secrete digestive ferments which are brought into contact with the food in the stomach.

The nervous system of the Mollusca (Fig. 124), in accordance with the absence of metamerism, lacks the ladder-like arrangement which characterizes the Annelida. Nevertheless there are two ganglionic masses, each in typical cases composed of two ganglia which may be homologized with the supraœsophageal and the most anterior subœsophageal ganglia of the metameric forms, and are known respectively as the *cerebral* (Fig. 124, *ce*) and *pedal* (*pe*) ganglia. The former lies above the œsophagus behind the buccal mass and is connected by nerve-cords termed connectives, surrounding the œsophagus, with the pedal ganglion. The cerebral ganglion gives off nerves which pass to the eyes and otocysts (*ot*) and to the tentacular structures of the head, while the pedal ganglion receives its name from the fact that it sends nerves to the muscular mass forming the foot. In addition to this system of nerves and ganglia there is another system highly developed in the Mollusca which would seem to correspond to the visceral system found in some other forms. It consists typically of a pair of *pleural* ganglia (*pl*), one of which lies upon either side of the pharynx, being united by connectives with both the cerebral and pedal ganglia. From each pleural ganglion a nerve-cord passes backwards to unite with one or more *visceral* ganglia (*vi*), situated below the intestine near its posterior termination, and on each of these visceral cords a ganglion occurs, the *parietal* ganglion (*pa*), from which nerves pass to the gills, or rather to the sense-organ which is in connection with them. The pleural ganglia innervate especially the mantle and the body-wall behind the head, the visceral ganglia send branches principally to the various viscera, while the parietal ganglia, in addition to the branches which go to the gills and their sense-organs, also assist in the innervation of the mantle.

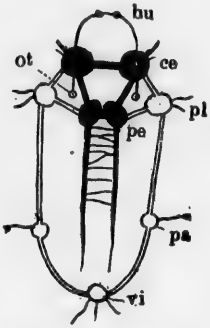

FIG. 124.—DIAGRAM OF NERVOUS SYSTEM OF MOLLUSK.

bu = buccal ganglia.
ce = cerebral ganglion.
ot = otocyst.
pa = parietal ganglion.
pe = pedal ganglion.
pl = pleural ganglion.
vi = visceral ganglion.

Besides these principal ganglia, however, others connected with either the cerebro-pedal or pleuro-visceral system may be developed, the most constant of which are the *buccal* ganglia (*bu*) which lie at the sides of or more usually below the buccal mass which they innervate and are united by commissures with the cerebral ganglia. Two nerve-rings in such cases surround the œsophagus, i.e., that formed by the cerebro-pedal and that of the cerebro-buccal connectives.

This description has reference only to what may be considered a typical condition, and it must be remembered that frequent modifications of it may occur. In the Gasteropods, for example, in which, in accordance with the development of a circular mantle-fold, the anus comes to lie on the anterior portion of the body-wall, a peculiar crossing of the pleuro-visceral commissures occurs in some cases, and as a result what was originally the right parietal ganglion comes to lie upon the left side of the body and the original left ganglion upon the right side. Further consideration of this arrangement may, however, be postponed until the Gasteropods are under discussion. Mention should, however, be made here of another not unfrequent modification of the typical arrangement of the nervous system, which consists in the concentration of the ganglia and the shortening of the various connectives. This may affect only the cerebral, pedal, and pleural ganglia, bringing them into close approximation, or, as in some Cephalopods, the visceral ganglia may also be carried forward so that all the principal ganglia are united into a single lobed mass closely surrounding the œsophagus behind the pharynx. This condition constitutes of course the culmination of the concentration process, but various gradations of it are to be found in the different groups.

Sense-organs are as a rule well developed in the Mollusca, and descriptions of many of them may be more conveniently given in connection with the detailed account of the various groups. The general ectoderm of the mantle and body-wall has scattered in it numerous sensory cells which may become specially aggregated at certain points to form definite sense-organs. Thus tentacles are frequently borne upon the head which are tactile or in some cases olfactory in nature, and at the bases of the gills special aggregations of sensory cells are to be found forming the *osphradia*, also supposed to have an olfactory function. Otocysts (Fig. 125) are present in nearly all the groups, consisting of a vesicle with a membranous wall, the interior of which is lined by sensory cells bearing bunches of hairs projecting into the vesicle which contains one or more calcareous otoliths. An auditory function has usually been attributed to these organs, but it seems probable that, as in the lower forms (see p. 82), they are rather to be regarded as organs of an equilibrium-sense, and in fact that they subserve such a function in part at least has been experimentally determined in the Cephalopods.

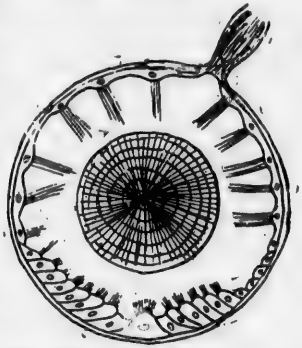

FIG. 125.—OTOCYST OF *Pterotrachea* (after CLAUS).

Eyes are very frequently present and in the Cephalopods reach an exceedingly high development. They occur usually upon the head, but may also be found, as in the Pelecypoda, upon the edge of the mantle, or even on the dorsal surface of the body, as in the Pulmonate *Onchidium*. They vary, however, so much in structure in different groups that an account of the various modifications which they present may be postponed.

Excretory organs in the form of a pair of nephridia are present, each nephridium consisting of a tube which opens at one extremity into the mantle-cavity, while at the other it communicates with the cavity of the pericardium, which, as has been seen, is a portion of the cœlom. The relationships of these structures are therefore the same as those of the nephridia of the Annelids, and, as in those forms, they receive a rich supply of blood, most of the venous blood returning from the tissues passing through their walls on its way to the branchiæ. The reproductive organs are unpaired in the majority of forms and in some cases come into relation with the nephridia, which serve as reproductive ducts. More usually, however, they open directly to the exterior, a condition which is probably a secondary one. The majority of the Mollusca are bisexual, but hermaphroditism is by no means uncommon, the single reproductive gland producing both ova and spermatozoa and being therefore an ovo-testis. Accessory structures are frequently added to the essential parts of the reproductive apparatus, such, for instance, as albuminiparous glands, intromittent organs, spermatophore-sacs, etc., so that a relatively complicated arrangement may occur.

I. CLASS **AMPHINEURA.**

The Amphineura are Mollusca in which the primitive bilateral symmetry is fully retained and which seem to approach most nearly to what may be considered the primitive Molluscan condition. All the known members of the group are marine in habitat and are more or less elongated forms in which the elongation of the ventral surface or foot is accompanied by a corresponding elongation of the visceral complex, which accordingly is not elevated at right angles to the long axis of the foot to form a visceral dome. In a general way, therefore, in the form of their body the Amphineura may be compared to the Platyhelminths, especially to such forms, sometimes flattened, sometimes more or less cylindrical and elongated, as are found among the Polyclad Turbellaria. The mouth and anus are situated at the extremities of the body, and to either side of the anus are situated the one or more pairs of plumelike branchiæ and the openings of the single pair of nephridia. The shell may consist either of a number of scattered calcareous spicules imbedded in or projecting from a thick cuticle, or else may take the form of a number of plates arranged in a longitudinal series upon the dorsal surface of the body, and as a rule the mantle-fold is but slightly developed and may be in some forms almost rudimentary. The foot, too, which is so characteristic for the Mollusca, may in some forms be practically undeveloped, but in other forms is a broad flat muscular surface, showing no differentiation into special regions such as are found in the higher Mollusca.

Little need be said here as to the internal organs except to emphasize the fact that both the heart and the nephridia have a perfectly bilateral arrangement. The nervous system is characterized by the absence of a definite aggregation of the nerve-cells into concrete ganglia; they are scattered along the longitudinal nerve-cords, of which there are two pairs, i.e., the pleuro-visceral cords, which run along the lateral portions of the body, and the pedal cords, which are situated more ventrally and which, as well as the pleuro-visceral, are frequently united by cross-commissures which suggest an imperfect metamerism. In front these cords unite together to form the circumœsophageal ring in which the ganglion-cells are somewhat more numerous than elsewhere, without, however, forming distinct ganglia. Sense-organs are but slightly developed throughout the group, which is divisible into two well-marked orders.

1. Order **Solenogastres.**

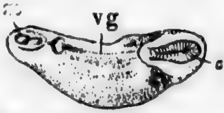

FIG. 126.—*Neomenia carinata* (after NANSEN).

ct = ctenidium.
m = mouth.
vg = ventral groove.

The members of this order are for the most part elongated worm-like animals, though some forms are short (Fig. 126) and more nearly approach the typical Molluscan form. The exterior of the body is covered by an exceptionally thick cuticle traversed by bands of cells extending into it from the ectodermal layer of the body and terminating in cup-shaped groups of cells which secrete the calcareous spicules which are scattered through the cuticle (*Proneomenia*) or may project upon its surface (*Chætoderma*), and which are the sole representatives of the shell of the higher Mollusca. Upon the ventral surface of the body is a longitudinal furrow (Fig. 126, *vg*) at the bottom of which lies the but slightly developed foot, represented by a small ciliated longitudinal ridge, which in *Chætoderma* may be quite undeveloped, the furrow being in this form also barely indicated or entirely absent. The lips of the furrow which enclose the foot probably represent the mantle-folds of higher forms, here very much reduced, though more extensively developed at the posterior end of the body, where they project to form a funnel-like structure (Fig. 127) whose cavity—the cloaca—receives the openings of the digestive tract (r) and the nephridia (n) and contains the branchiæ (ct). These last are either a single pair of structures each consisting of a central axis with pinnately-arranged lateral appendages or in some cases are represented by bunches of ciliated filaments.

The ectoderm rests upon a layer of muscular tissue in which both circular and longitudinal layers can be distinguished, and numerous bands of transverse fibres, in some cases arranged to form septa placed at regular intervals, traverse the body-cavity. A fairly-capacious pericardium is present, lying dorsally to the posterior portion of the digestive tract and into its upper portion the heart projects slightly, not being, however, completely enclosed by the pericardium. No auricles seem to be developed, nor are any definite blood-vessels present, the circulation being throughout lacunar.

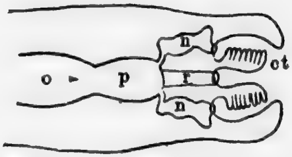

FIG. 127.—DIAGRAM OF ARRANGEMENT OF ORGANS AT HIND END OF *Chætoderma* (after HUBRECHT from LANKESTER).

ct = ctenidium.
n = nephridium.
o = ovary.
p = pericardium.
r = rectum.

This condition of the heart in relation to the pericardium is interesting as showing its original independence of that portion of the body-cavity. Its enclosure in the pericardium in the higher Mollusca is a secondary condition, the heart and its cavity belonging to the schizocœlic structures rather than to the so-called enterocœlic pericardium. This agrees perfectly with the relationships of the blood vascular system of the Nemerteans and Annelids. (See pp. 165 and 231.)

The mouth is a longitudinal slit upon the ventral surface of the body and opens into a pharynx provided usually with a radula and with salivary glands, though both these structures are absent in *Neomenia.* The intestine pursues a straight course towards the anal opening, being, however, in some forms pouched, owing to its constriction at more or less regular and close intervals by muscular transverse septa. The walls of the pouches thus formed are glandular and represent the digestive gland of other Mollusca, though in *Chætoderma* there is a simple outgrowth of the digestive tract which represents it more perfectly.

The nervous system varies in the details of its arrangement in the different species, but is characterized in general by a tendency to form ganglia, although nerve-cells are scattered along the nerve-cords throughout their entire length. In *Proneomenia* there is present a well-developed and closely-approximated pair of cerebral ganglia from which arise the pleuro-visceral cords which extend backward along the sides of the body and possess a number of ganglionic swellings near their posterior extremity. Two nerve-rings surround the œsophagus: (1) the cerebro-pedal connectives, which end below in the pedal ganglia, from which two pedal cords extend backward along the foot, in some forms (*Dondersia*) connected at regular intervals by transverse commissures in an almost metameric manner, ganglionic enlargements of the cords being developed in connection with the commissures; and (2) the cerebro-buccal connectives, which pass to two buccal ganglia lying below the pharynx. Special sense-organs have not yet been discovered in the Solenogastres.

The nephridia consist of a pair of tubes which communicate internally with the pericardial cavity and, bending around the posterior part of the digestive tract, unite to open into the cloaca ventral to the anus by a common orifice. The walls of the tubes are glandular and probably, therefore, excretory in function, but the nephridia also serve as the ducts for the reproductive elements. With the exception of *Chætoderma* the Solenogastres are hermaphrodite, the single reproductive

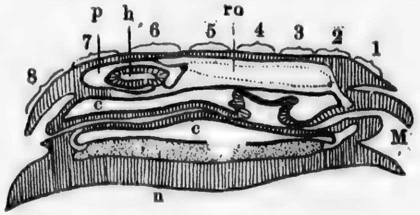

FIG. 128.—DIAGRAMMATIC LONGITUDINAL SECTION OF *Chiton* (after HALLER).

c = perivisceral cœlom.
n = nerve.
h = heart.
p = pericardium.
m = mouth.
ro = reproductive organ.
1–8 = shell-plates.

gland producing both ova and testes. This hermaphrodite gland is a hollow sac divided into two principal compartments by a longitudinal partition and lies above the digestive tract. It is a hollow structure (Fig. 128, *ro*), the reproductive elements developing from the cells lining its walls and passing from its cavity into that of the pericardium (*p*), with which the reproductive sacs communicate. They are in fact simply prolongations of the pericardial body-cavity, and the epithelium lining them is continuous with that of the pericardium. From the pericardial cavity the ova and spermatozoa pass to the exterior by the nephridia.

The Solenogastres are especially interesting on account of the many structural peculiarities of a primitive character which they present and in consequence of which they have been regarded as representatives of ancestral Molluscan forms. By others, however, this important position is denied them on the ground that many of their peculiarities are due to degeneration produced in accordance with their life in the mud at the bottom of the ocean. The absence of a shell, the reduction of the mantle-lobes, foot, and radula may with plausibility be accounted for in this manner, but there are other peculiarities that are certainly primitive which are not thus explicable. The relation of the heart to the pericardium is one of these, and others are the communication of the hermaphrodite gland with the pericardium, and the functioning of the nephridia as ducts for the reproductive organs. The Solenogastres are unquestionably primitive Mollusca; the only question which is yet to be settled is to what extent, if any, degeneration is responsible for their external peculiarities, such as the absence of a shell, the reduction of the mantle-lobes and of the foot. It must be noted in this connection that one form belonging to the genus *Dondersia* has been described as passing through in its development a stage in which indications of a shell consisting of several plates and similar to that of the Polyplacophora was present, a condition which would seem to indicate the derivation of the members of this group from forms provided with a distinct shell.

2. Order **Polyplacophora.**

The Polyplacophora, like the preceding order, contains only marine forms. For the most part they are somewhat flattened animals with a rather broad foot occupying the ventral surface, while from the sides of the body a slight fold, the mantle-fold, projects. In one genus, *Chitonellus*, the form of the body is more cylindrical and the foot is rather narrow and situated, as in the Solenogastres, at the bottom of a median ventral furrow, the lips of which correspond to the more dorsally situated mantle-folds of such forms as *Chiton*, *Trachydermon* (Fig. 129), etc. In all cases, in the groove between the mantle-folds and the foot a number of gills, pinnate processes of the body-wall, are to be found, in some cases occurring at definite intervals along the entire side of the body, in others (*Chitonellus*) limited to the posterior part only.

One of the most characteristic features of the Polyplacophora is, however, the shell, which consists of eight calcareous plates arranged in a longitudinal series along the dorsal surface of the body so that the posterior border of one overlaps the anterior border of the other. The series covers only the median portion of the surface, the more peripheral portions and the outer surface of the mantle-lobes possessing a large number of scattered spicules, plates or granules imbedded in their wall.

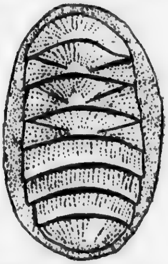

Fig. 129.—*Chætopleura apiculata.*

The body-wall has not so definite an arrangement of the muscle-fibres lying below the ectoderm as is the case in the Solenogastres, but, on the other hand, the body-cavity is well developed. Indeed the schizocœlic lacunæ play a rather subordinate part in the Chitonidæ, as the order is sometimes termed, the enterocœlic cavity (Fig. 128) being very large and divisible into three usually separated parts united by bands, which indicate the original continuity. One of the parts (*c*) surrounds the intestine and the digestive gland; another, lying rather towards the anterior end of the dorsal portion of the body, contains the reproductive cells (*ro*); while the third part (*p*), lying dorsally and posteriorly, is the so-called pericardium.

The two auricles of the heart are elongated tubes which communicate with the single ventricle by one or several pairs of openings and also unite together posteriorly, the ventricle, also an elongated tube, sometimes again communicating with this united portion. Anteriorly the ventricle is continued into a short aorta from which the blood passes to the lacunar spaces of the schizocœl. Two vessels with distinct walls run longitudinally in the foot, and presumably receive the blood which they contain more or less directly from the aorta and distribute it to the lacunar spaces of the foot.

The mouth lies on the ventral surface, in front of the anterior end of the foot, and leads into a pharynx provided with a well-developed radula characterized by a somewhat complex arrangement of the teeth. Into the œsophagus a pair of glands opens in *Chiton* whose secretion contains an amylolytic ferment, and in addition a pair of small glands open into the mouth-cavity. The œsophagus communicates with a sac-like stomach, into which open the ducts of the paired digestive gland, and the intestine, being considerably longer than the body, is thrown into numerous coils, and terminates by a short rectum which opens at the posterior extremity of the body.

The nervous system is characterized by the diffuse arrangement of the nerve-cells, no well-defined ganglia occurring on the principal nerve-cords. These consist of a strong circumœsophageal ring (Fig. 130), the upper part of which gives off numerous nerves and evidently corresponds to the cerebral ganglia of other Mollusca, while the lower part, corresponding to the pedal ganglia, gives rise to two nerve-cords (*pc*), the pedal nerves, which pursue a parallel course throughout the foot, giving off a number of nerves laterally and being connected by a number of somewhat irregularly arranged transverse commissures, which almost suggest a metameric arrangement. From the sides of the circumœsophageal ring two other strong nerves, the pleuro-visceral nerve-cords, arise and pass backwards along the sides of the body, uniting with each other posteriorly above the terminal portion of the digestive tract. These cords (*pl*), like the circumœsophageal ring, present no distinct ganglionic enlargements, but contain the elements of the pleural, visceral, and parietal ganglia, sending off numerous nerves to the branchiæ, the mantle, and probably also to the heart and nephridia.

In addition to these principal nerve-cords others of smaller size also arise from the circumœsophageal ring. One pair of these pass to a pair of ganglia, the buccal ganglia, lying beneath the buccal mass and send nerves to the œsophagus while another pair pass to a pair of ganglia lying below the radula and in intimate connection with a peculiar subradular organ, probably sensory, lying in this region.

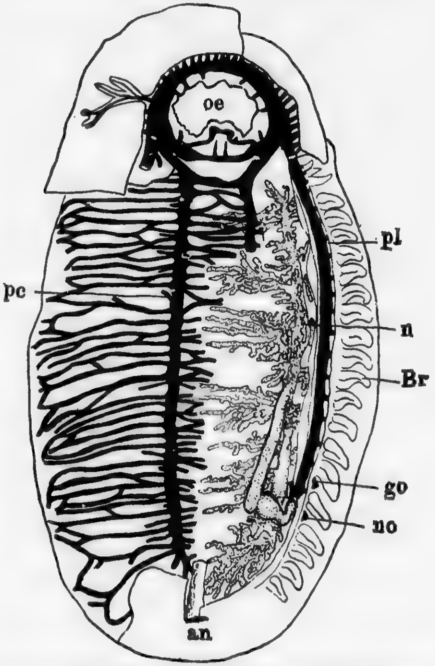

FIG. 180.—DIAGRAM OF NERVOUS AND EXCRETORY SYSTEMS OF *Chiton siculus* (combination of two figures by HALLER).

an = anus.
Br = ctenidia.
go = genital orifice.
n = nephridium.
no = nephridial orifice.
oe = œsophagus.
pc = pedal nerve-cord.
pl = pleural nerve-cord.

As regards sense-organs, in addition to this subradular organ whose function is entirely problematical, ridges of sensory epithelium exist along the sides of the body in the mantle-cavity. One such ridge runs along the inner wall of the mantle-fold, while the other is found at the bottom of the mantle-cavity passing over the bases of the branchial plumes and sending a short prolongation outwards upon each of these structures and seeming thus to correspond with the osphradia of other Mollusca.

A much more peculiar series of organs, found, however, in their perfect form only in certain species, is developed in connection with the shell of the Chitonidæ. They consist of club-shaped structures contained in pores which traverse the shell-plates and possess a definite arrangement, being arranged in groups of larger and smaller organs (*megalœsthetes* and *micrœsthetes*). Each group is in connection with a number of large glandlike cells, which terminate in the megalæsthete, covered externally by a cup-shaped layer of chitin, and from this cell-mass more or less numerous branches arise, the micræsthetes, which terminate in club-shaped swellings likewise covered by a chitinous layer. Below the group of cells is in connection with fibrils which unite to form a nerve probably passing to the pleuro-visceral nerve-cords, and it thus seems tolerably certain that these structures are sensory and perhaps tactile in function. In some species the megalæsthetes become modified into eyes consisting of an external convex chitinous cap, the cornea, below which is a lens and below this a layer of retina-cells connected with nerve-fibrils and surrounded by a cup of pigment-cells. No eyes other than these occur in the Polyplacophora, nor are tactile tentacles or otocysts, of such frequent occurrence in other Mollusca, found.

The nephridia (Fig. 130, *n*) are paired, one lying on each side of the body and consisting of a long tube giving rise to numerous dendritic branches. Posteriorly the tube branches, one of the branches opening into the mantle-cavity in its posterior part, while the other communicates with the pericardial portion of the enterocœl. In function these organs of the Chitonidæ differs from the corresponding ones of the Solenogastres in being excretory only and in not serving as ducts for the reproductive elements. These are developed in a portion of the enterocœl which lies anteriorly to the pericardium and make their way to the mantle-cavity and so to the exterior by special ducts arising one on each side from near the posterior part of the reproductive enterocœl and ending (*go*) on the sides of the body slightly in front of the openings of the nephridia (*no*). The Polyplacophora are without exception bisexual.

The structural peculiarities of the Polyplacophora point strongly to their primitive character, though in many respects they are less primitive than the Solenogastres. Thus they possess special reproductive ducts, in all probability a secondary acquisition, and furthermore the reproductive and pericardial moieties of the enterocœl no longer communicate freely. If the Solenogastres have been derived from forms with Chiton-like shells (see p. 288), then it must be supposed that the two groups represent diverging lines of development from a common ancestor whose characteristics have been partly retained in the one group and partly in the other.

II. Class **Gasteropoda.**

The Gasteropods form a very complex group, the various members differing so much in the details of their organization that it is difficult to give a general description which will apply to all the forms. Certain features may, however, be considered typical of the class, and these may be mentioned here, reserving notice of the more important variations until the various subdivisions are being considered.

One of the most characteristic features is the occurrence of what may be termed the "visceral hump" whose presence is responsible for many of the peculiarities of Gasteropod structure. It consists of an elevation into a dome-like structure of the dorsal region of the body, the digestive tract and gland being contained within the elevation. The mantle arises as a circular fold surrounding the hump, but usually is more highly developed, and therefore encloses a deeper cavity, upon the right side or anterior surface of the hump, and in the cavity so arranged lie the structures which usually are associated with the mantle-cavity, namely, the branchiæ and the openings of the digestive tube and of the nephridia. There is thus a very decided asymmetry in most Gasteropods, usually emphasized by the visceral hump being coiled into a spiral, a coiling which is shared by the shell, usually present and consisting of a single tubular structure surrounding the visceral hump, but usually sufficiently ample to permit of the retraction within it of the rest of the body.

In a number of forms the visceral hump may be very much reduced, and with this reduction there is generally concomitant a reduction of the shell, but such conditions are plainly secondary inasmuch as the primitive asymmetry is indicated in certain of the organs in all cases. In order to understand the exact nature of this asymmetry it will be necessary to consider what may have been the original form of the Gasteropoda. Judging from what is known of the Amphineura, it may be supposed that in the primitive Gasteropod (Fig. 131, *A*) the anus (*a*) was terminal and opened into a mantle-cavity, the mantle being, except posteriorly, only a slight fold. In this mantle-cavity there was present also a single pair of branchial plumes (*ct*), and into it the two nephridia opened (*n*), passing from the posteriorly-situated pericardium which contained the heart provided with two auricles.

It may be imagined now that in such a form the visceral hump enclosed by a dome-like shell became elevated to such an extent that it could no longer be retained in an erect position, but fell over to one side—it may be supposed the left side. The result of this would be an interference with the development of the mantle-cavity towards the left side, and a prevention of the perfect growth of the left branchia and of the proper functioning of the left nephridium. There would be a tendency then for the mantle-cavity, and with it the anus and indeed the entire posterior region of the body with the heart and nephridia, to be pushed over towards the right side (Fig. 131, *B*), and this process might in some cases be continued until the mantle-cavity and the organs associated with it had been pushed round through 180° (Fig. 131, *C*, *D*) and had come to lie apparently in front of the visceral hump (*D*). The anus in such a case would open into the mantle-cavity in the mid line, dorsal to the mouth, and what was originally the right branchia would lie upon the left side of the body; the digestive tube, which may originally have been practically a straight tube, would now be bent upon itself, and furthermore the original right parietal nerve-ganglion would have passed over to the left side of the body and the original left ganglion to the right side, a crossing of the pleuro-parietal connectives (*vc*) being thus brought about.

The original pressure of the shell upon the left half of the mantle-cavity would, however, as pointed out, have tended to produce a retardation in the growth or even the complete abortion of the organs lying in that region. Accordingly the original left nephridium is in many Gasteropods completely suppressed as well as the original left branchia, and in accordance with the disappearance of this latter structure there is a disappearance also of the left auricle of the heart which receives blood from it.

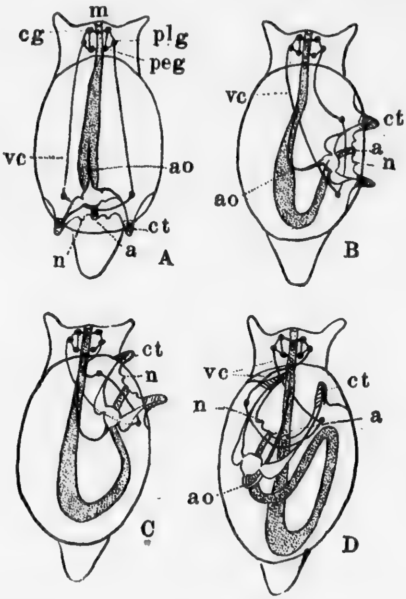

FIG. 131.—DIAGRAMS TO ILLUSTRATE THE ROTATION OF THE MANTLE-CAVITY AND ITS ORGANS IN A GASTEROPOD (after figures by BÜTSCHLI and LANG from KORSCHELT and HEIDER).

a = anus.
ao = aorta.
ct = ctenidium.
cg = cerebral ganglion.
m = mouth.
n = nephridial pore.
peg = pedal ganglion.
plg = pleural ganglion.
vc = visceral connective.

The visceral hump does not, however, retain its original conical form, but, owing perhaps to unequal pressure, grows more rapidly upon one surface, the anterior, and so becomes coiled into a right-handed spiral, the shell covering the hump naturally assuming a similar form. In the majority of

Gasteropods consequently a shell coiled in a right-handed spiral occurs, but this rule has not a few exceptions. Where the shell forms a left-handed spiral it is to be explained by supposing that in such cases the visceral hump tended towards the right side of the body rather than the left, and this is confirmed by the fact that in most left-handed forms it is the *left* branchia and nephridium that have persisted.

It must be pointed out, however, that the extent to which the rotation of the mantle-cavity, the abortion of the organs of either the left or right side of the body, and the crossing of the pleuro-parietal nerve-cords has been carried varies in different forms. In some the rotation has been carried so far that the original right branchia, etc., has passed the median line in front so as to lie on the left side of the body, and in such cases the crossing of the nerve-cords (chiastoneurism) is completed. Many forms, however, stop short of this, and numerous gradations are to be found. The rotation, however, is present in all forms to some extent and forms a characteristic feature of Gasteropod morphology.

The anterior portion of the body (Fig. 132) is usually well marked off by a more or less distinct constriction or neck, and consequently it is possible in the Gasteropods to speak of a head in contradistinction to the trunk region of the body; indeed so prevalent is this character that the term *Cephalophora* has been applied to the group. Tentacles, either one or two pairs, are borne by the head, and furthermore eyes are usually present upon it either at the bases of one of the pairs of tentacles or else borne at the tips of these structures.

The foot is generally well developed and usually has a flat creeping sole. It undergoes many modifications, however, sometimes becoming more keel-like, or becoming differentiated into three regions differing in form, the propodium, mesopodium, and metapodium, the last-named portion frequently secreting a chitinous plate, the operculum (Fig. 132, *op*), which serves to close the mouth of the shell when the animal is withdrawn within it. In addition to these portions an epipodium is frequently highly developed, consisting in its primitive form of a fold arising from the sides of the foot where it passes into the body-wall. In many cases, however, it loses this simple form, its margin becoming fringed or tentaculate, or else it may be reduced to one or more separate lobes or tentacular processes on either side of the body. Opening upon the surface of the foot is frequently to be found a so-called "foot-gland" which secretes a sticky mucous fluid and is comparable to the byssus-gland of the Pelecypoda (*q. v.*).

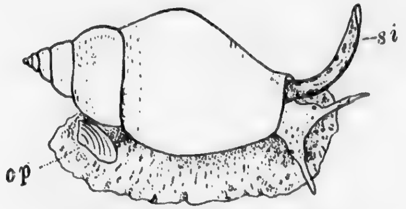

FIG. 132.—*Buccinum undatum.*
op = operculum. *si* = sipho.

The respiratory organs (Fig. 133, *ct*) consist in typical cases of a single pair of pinnate branchial plumes lying in the mantle-cavity, but, as has already been mentioned in connection with the rotation of that cavity, one of these structures is very frequently aborted. Other changes, however, also occur, such, for example, as the fusion of the central axis of the branchial plume throughout its entire length to the inner surface of the mantle (*Haliotis*), or the disappearance of the pinnæ from one side of the plume in connection with such a fusion (*Sycotypus*, Fig. 133). In some forms accessory branchiæ may be produced as folds of the mantle, richly supplied with blood, and their development may be carried to such an extent that they may entirely supplant the branchiæ proper (*Patella*). From such a condition as this a passage is not difficult to such a condition as is found in the air-breathing Gasteropods (Pulmonata) in which the entire inner surface of the mantle serves a respiratory purpose, an interchange of gases taking place between the air contained in the mantle-cavity and the blood which is richly supplied to the mantle.

The musculature of the body-wall does not as a rule present the Annelidan arrangement in layers, as in some Amphineura, but usually are irregularly arranged as dorso-ventral and oblique bands traversing the schizocœl. Special muscles, however, are developed in many forms, the most important being those connected with the foot and serving for locomotion, retractor muscles in connection with the head, proboscis, and tentacles, and the spindle-muscle, which has a general vertical direction running along the right side of the visceral hump from its insertion into the shell to the foot in whose wall its fibres spread out, interlacing as it were with the horizontal and transverse muscles there developed; it serves to retract the entire animal within the shell, and its development is naturally in proportion to that of the shell, those forms in which the shell is rudimentary or absent frequently lacking it.

The enterocœlic portion of the cœlom is much reduced in comparison with what occurs in the Amphineura, being distinctly represented only by a comparatively small pericardium surrounding the heart, the auricle in some cases not being enclosed by it. From analogy with the Amphineura, however, the reproductive organs must be regarded as representing a portion of the enterocœl whose connection with the pericardium has been completely severed. A glandular structure, the pericardial gland, is in some Gasteropods developed by the folding of the pericardial walls, and has apparently an excretory function acting as an accessory nephridium; it is not, however, as highly developed as in some of the other Molluscan groups.

The circulatory organ possesses in some forms the characteristic Molluscan structure, consisting of an unpaired ventricle lying in the pericardium and receiving the blood from two lateral wing-like auricles. In many cases, however, as already pointed out, the asymmetry produced by the development of the visceral hump affects the heart, resulting in the suppression of one of the auricles, that of the left (or right) side (Fig. 133). In such cases the persisting auricle may secondarily assume a terminal position with regard to the ventricle, and the latter, instead of being continued into an artery at either extremity, gives off a single artery at the end opposite to that at which the blood enters from the auricle, this artery dividing into two main trunks which distribute the blood to the various regions of the body. These arteries may be continued as distinct tubes with definite walls for some distance from the heart, but sooner or later the blood passes into the system of lacunar spaces constituting the schizocœl, whence it is again returned to the auricle through a series of veins. The position of the single auricle with reference to the body axis differs in different orders of Gasteropods, in accordance with the varying position of the branchia. In those forms in which the branchia lies in front of the heart the auricle lies at the anterior end of the ventricle, while when the branchia is posteriorly situated the auricle lies behind the ventricle.

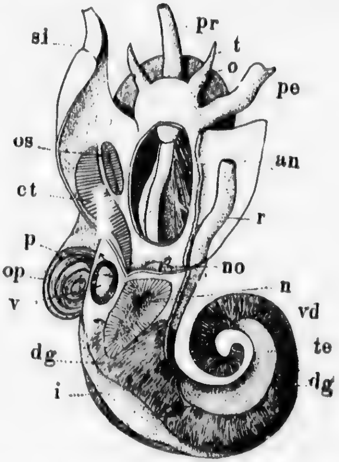

FIG. 133.—STRUCTURE OF *Sycotypus canaliculatus.* The mantle is divided in the middle line and turned aside, exposing the mantle-cavity.

an = anus.
ct = ctenidium.
dg = digestive gland.
i = intestine.
n = nephridium.
no = nephridial opening.
o = eye.
op = operculum.
os = osphradium.
p = pericardial cavity.
pe = penis.
pr = proboscis.
si = sipho.
t = tentacle.
te = testis.
v = ventricle.
vd = vas deferens.

The arrows show the openings of nephridium to the mantle-chamber and to the pericardium.

The mouth lies in all Gasteropods at the anterior extremity of the body, towards the ventral surface of the head, and opens into a mouth-cavity frequently provided with two or more chitinous teeth. The pharynx usually receives the ducts of a pair of salivary glands, contains a well-developed radular organ in practically all cases, and communicates posteriorly with a tubular œsophagus. In many cases the anterior portion of the digestive tract is capable of being protruded as a proboscis (Fig. 133, *pr*), which lies when retracted within a proboscis-sheath, formed by a circular infolding of the body-wall around the mouth. The intestine (*i*) is usually more or less coiled, extending into the visceral hump, and presents a stomach-like enlargement which receives the ducts of the digestive gland (*dg*), a structure usually well developed and forming the greater portion of the visceral hump. The intestine terminates in a straight portion, the rectum (*r*), which passes forward to the anus (*an*), which, as has already been indicated, lies in the mantle-cavity, slightly to the right, but occasionally to the left, of the middle line, its position depending upon the amount of rotation which the mantle-cavity and the associated organs have undergone. It should be mentioned that in one suborder of Gasteropods the pericardium and ventricle have wrapped themselves around the rectum in such a way that the digestive tube seems to have penetrated the ventricle, a feature which will later be seen to be characteristic of one of the other groups of Mollusca.

The nervous system has the arrangement which has been described as characteristic of the Mollusca (Fig. 124), the peculiar feature being the crossing of the pleuro-parietal connectives which is found in many forms. Numerous modifications of the typical condition are to be found, consisting principally in (1) the concentration of the ganglia, more especially the cerebral, pleural, and pedal, or the pedal, pleural, parietal, and visceral (Fig. 139), to form a single mass; (2) in the suppression in some cases of one of the parietal ganglia; and (3) in the occurrence of several visceral ganglia. In accordance with the flat elongated form of the foot in many species, the nerve-cords passing backward from the pedal ganglia may be of considerable size, and furthermore may be connected by regularly-arranged transverse commissures, recalling the condition seen in the Chitons, as well as the ladder-like arrangement of the ventral nerve-cords of the Annelida, though there cannot in the Gasteropods be any question of metamerism in this connection.

Special sense-organs are very generally well developed in the Gasteropods. The tentacles so usually found upon the head have probably a tactile function as well as the tentacular or winglike processes sometimes found in connection with the anterior extremity of the foot, and the epipodial tentacles which occur in some forms (*Haliotis*). On the ventral side of the bases of the epipodial tentacles of some forms special sensory thickenings have been found which have suggested a comparison with the sense-organs of the lateral line of the Annelida, a comparison which, however, at present seems rather strained; it seems probable, notwithstanding their innervation from the pedal ganglia, that these sensory patches are to be placed in the same category as the osphradia and the sensory ridges of the mantle-cavity of the Chitons. The osphradia (Fig. 133, *os*) in all Gasteropods which are provided with branchiæ are associated with these organs; and even where one or both branchiæ have been suppressed the osphradia may still persist. Eyes (Fig. 134) are very generally present in the Gasteropods, being situated at the base of the tentacles, or at their summit in some forms. They present a very uniform structure throughout the group and arise as a depression of the integument, the lips of the cavity fusing and giving rise to a globular sac lying beneath the epidermis, which remains thin and transparent, forming an outer cornea (*co*). The cells of the outer wall of the sac likewise remain clear, forming the inner cornea, while over the remainder of the wall of the sac they are sensory in function, pigmented cells being scattered among them, the two together forming the retina (*ret*). The nerve-fibres pass-

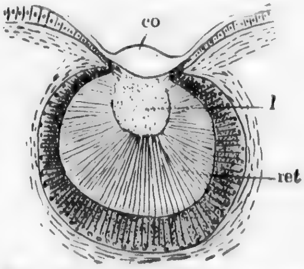

FIG. 134.—EYE OF *Haliotis* (after PATTEN).

co = cornea.
l = lens.
rt = retina.

ing to the eye from the cerebral ganglia pass through an optic ganglion lying beneath the optic sac and are distributed to the sensory cells, and the centre of the sac is filled up by a cuticular mass which serves as a refractive lens (*l*). In some forms (*Patella*, etc.) the development of the eye ceases while it is still in the cup form, there being then no formation of corneal layers and no central lens, though the retina is usually covered by a thin cuticular layer. In some species of a peculiar genus of the air-breathing Gasteropods, *Onchidium*, eyes are developed upon the dorsal surface of the body, the shell being lacking and the visceral hump undeveloped. In structure these eyes differ very materially from those usually occurring in the Gasteropoda and will be described later (p. 318).

Otocysts are usually imbedded in the tissues of the foot close to the pedal ganglia, though in all cases they receive their innervation from the cerebral ganglia; they have the usual sac-like form and are lined with sensory hair-bearing cells and contain otoliths.

The nephridia of the Gasteropods are in nearly all cases modified from the original typical condition in accordance with the asymmetry of the body (Fig. 133, *re*). In only a few forms, so far as known (*Fissurella*, *Patella*), are two functional nephridia, opening on the one hand into the pericardial cavity and on the other to the exterior through the mantle-cavity, perfectly developed. In other forms, such as *Haliotis*, *Turbo*, etc., both nephridia are present and are structurally perfect, though the left[*] one has lost its secretory function, but in the majority of cases the left (or, in forms with a left-handed coiling of the visceral hump, the right) nephridium is completely aborted.

The Gasteropods are in some cases bisexual, in others hermaphrodite. The reproductive sac (Fig. 133, *t*) is quite unconnected with the pericardial enterocœl and is an unpaired structure lying in the visceral hump. The ova and spermatozoa in most cases reach the exterior by a special duct (*vd*), having apparently no relation to the nephridia and opening into the mantle-cavity to the right side of the anus. In the more primitive Gasteropods, however, such as *Haliotis*, *Fissurella*, and *Patella*, the nephridia, as in the Solenogastres, serve as reproductive ducts; and it has been suggested that the special reproductive duct of the remaining Gasteropods may represent the left nephridium, which is usually described as having disappeared. The reproductive duct, especially in hermaphrodite forms, has developed in connection with it accessory glandular structures as well as external copulatory organs, the whole reproductive system becoming highly complicated. An account of the more important arrangements will be more satisfactorily given in connection with the various orders.

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[*] The terms left and right refer to the position of the nephridia as they are supposed to have been arranged in the primitive symmetrical Gasteropod.

1. Order **Prosobranchia.**

The Prosobranchia are, with very few exceptions, marine Gasteropods, provided with well-developed shells, which are usually spirally coiled, the height of the spiral varying, however, in different forms. In some, such as *Patella* and *Fissurella*, the shell has a simple conical form, without any indication of a spiral; and since these forms in many respects show primitive characters, it might be supposed that this type of shell was also primitive. These very forms, however, show also that asymmetry of parts, which is characteristic for the Gasteropods, and which accompanies the rotation of the mantle-cavity, and furthermore, in *Fissurella* at least, a distinct indication of a spiral coiling, is present in the shells of young animals. It seems more probable, accordingly, that these conical shells are to be regarded as secondary modifications of an originally spirally-coiled shell.

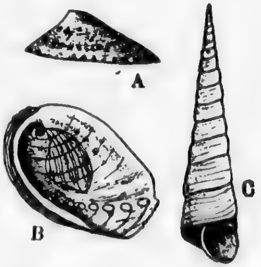


FIG. 185.—SHELLS OF PROSOBRANCH GASTEROPODS. *A*, *Acmæa testudinalis* (after GOULD); *B*, *Haliotis* (after LEUNIS); *C*, *Turritella* (after LEUNIS).

The mantle-cavity is situated in front of the well-developed visceral hump, and is usually somewhat capacious, communicating with the exterior freely. In some forms the mantle is slit from its margin upwards and backwards, a corresponding slit occurring in the shell (*Emarginula*). In *Haliotis* and *Pleurotomaria* the slit in the shell becomes closed at regular intervals, producing a row of round perforations, beneath which lies the mantle-slit, and through which water finds a ready exit from the mantle-cavity, and, in *Fissurella*, in which at an early stage the margin of the shell possesses a slit, by the subsequent growth and obliteration of the spiral coiling the slit becomes converted into an aperture which lies almost at the apex of the conical shell and leads into the mantle-cavity, functioning as a means of exit of the water and excrementa from that cavity. In the greater number of forms, however, such slits or apertures do not exist; but one finds frequently the margin of the mantle produced at one point on the left side into a projecting narrow lobe whose edges may be brought into opposition, thus producing a tube or siphon through which water may pass into the mantle-cavity. Where this siphon is well developed a distinct notch is found in the margin of the shell, through which it may be protruded, or else the lips of the notch are prolonged so as to form a grooved process, the siphonal canal, in which the siphon lies, being by these arrangements able to function even when the mouth of the shell is closed by the operculum. In many forms the mantle-folds are sufficiently large to allow of their being reflected over the outer surface of the shell when the body is fully protruded.

The foot is as a rule adapted for creeping, but in many cases is differentiated into pro-, meso- and metapodium, the last usually bearing a chitinous or more or less calcified operculum. In certain forms belonging to a group of pelagic forms, however, which were formerly associated together as a distinct order, the *Heteropoda* (Fig. 138), the pro- and mesopodium are modified into a keel-like structure and bear a peculiar sucker. The epipodium is frequently developed in the Prosobranchia, especially in the more primitive species—most frequently, however, being reduced to tentacle- or lobe-like processes arising from the sides of the foot.

In the majority (Fig. 133) of forms there is but a single branchia which lies in front of the heart, whence the name of the order, but in a few genera the original left gill also persists. In many forms a gland is developed in the floor of the mantle-cavity close to the rectum—hence called the adrectal gland—which in some forms, e.g. *Murex* secretes a purple pigment. The rotation of the mantle-cavity and the associated organs has called forth a crossing of the pleuro-parietal nerve-cords, a feature which is lacking in the other orders and therefore forms a characteristic of the Prosobranchs.

In all but a few cases the members of the order are bisexual, the unpaired reproductive gland lying in the visceral hump. The oviduct has in connection with it one or more receptacula seminis and dilates into a glandular uterus in which the eggs are supplied with the albumen in which they are usually imbedded and also surrounded by a shell. In the males, except in the more primitive forms, there is present a well-developed intromittent organ or penis (Fig. 133, *pe*), situated upon the right side of the head or neck and therefore removed at some distance from the opening of the vas deferens into the mantle cavity. A groove or tube extends, however, from the reproductive orifice to the grooved or tubular penis, and along this groove or tube, by the ciliary action of the cells lining it, the seminal fluid is carried.

1. Suborder *Diotocardia.*

This suborder includes the more primitive Prosobranchs, in which, although a considerable rotation has occurred, yet nevertheless the abortion of the organs of the original left side of the body has not been carried very far. Thus, except in *Patella* and some allied forms, there are two auricles to the heart, although in *Turbo, Trochus, Neritina*, and allied genera that of the right side (i.e., the original left one) does not communicate with the ventricle. Attention may again be called to the fact that in those forms which possess two functional auricles the ventricle and pericardium have wrapped themselves round the rectum which seems to perforate the ventricle. Such forms as *Haliotis, Fissurella*, and *Pleurotomaria* possess two branchiæ, but in the majority of the members of the group only one is present, while in *Patella* both have disappeared, their place having been taken by respiratory folds of the mantle. Both kidneys are invariably present.

The primitive character of the suborder is further shown in the absence of certain structures found in more specialized forms. Thus the foot is flat and undifferentiated into pro-, meso-, and metapodium; the anterior part of the digestive tract is not evertible as a proboscis; there is no siphonal prolongation of the mantle, and no notch or siphonal groove on the margin of the shell; and there is no penis. On the other hand the epipodium is usually well developed, as are also the pedal nerve-cords, which are connected by numerous cross-commissures.

A further distinguishing feature of the suborder is the arrangement of the teeth of the radula. Each transverse row of teeth presents an indefinite number of marginal teeth, usually a single lateral, a single median, and a varying number of admedian teeth, an arrangement known as rhipidoglossate. Thus in *Haliotis* the arrangement is indicated by the formula x, 1, 5, 1, 5, 1, x; in *Fissurella* by x, 1, 4, 1, 4, 1, x; and in *chus* (Fig. 136) and *Turbo* by x, 0, 5, 1, 5, 0, x, the single lateral tooth being absent in these forms. In *Patella*, however, another arrangement is found characterized by the occurrence of only a small number of marginal teeth and by the absence of the median, the formula being 3, 1, 2, 0, 2, 1, 3; this arrangement is termed docoglossate.

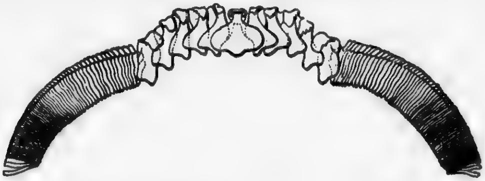


FIG. 136.—DENTITION OF *Trochus* (after LANKESTER).

2. Suborder *Monotocardia*.

In this suborder the effect of the pressure of the visceral hump on the organs of the left side of the mantle-cavity is more pronounced than in the Diotocardia. The heart possesses a single auricle only, except in *Cypræa*, where the rudiment of a second occurs, and throughout the group but a single nephridium is present. There is never more than a single gill, which is usually more or less united to the mantle-wall and bears lateral branches only upon one side.

The foot is in some cases flat and broad, as in the Diotocardia, and in such cases may possess the parallel pedal nerve-cords with transverse commissures as in *Cypræa* and *Paludina*, but usually it becomes more or less differentiated, a propodium being in many cases well defined (*Strombus*, *Natica*), while a chitinous or calcareous operculum is usually carried by the metapodium, and the pedal nerve-cords are very much reduced or wanting, the pedal ganglia being on the other hand more highly developed than in the Diotocardia. The epipodium is usually entirely wanting, and when present is but slightly developed, reaching its fullest development as a continuous fold upon the sides of the foot only in *Ianthina*. In *Paludina* it is represented by two anteriorly-situated tentacle-like lobes, and in *Calyptræa* by a semicircular fold on each side of the neck region.

The Monotocardia are further distinguished by the frequent occurrence of a well-developed siphon and a more or less developed siphon groove at the margin of the shell, and furthermore a well-developed penis is usually present.

The anterior portion of the digestive tract is in many forms capable of being protruded as a proboscis. The arrangement of the teeth of the radula varies considerably in different forms, but the rhipidoglossate arrangement is not represented. In one group, including the genera *Cypræa*, *Natica* (Fig. 137, *A*), *Littorina* (the periwinkles), *Calyptræa*, *Strombus*, etc., the tænioglossate arrangement is found, represented by the formula 2 or 3, 1, 1, 1, 2 or 3, the admedian teeth, however, being very similar to the lateral. In other cases but a single median tooth or the median with a single admedian on each side is found, as in *Fusus*, *Buccinum* (the whelks), *Nassa* (Fig. 137, *B*), *Murex*, *Purpura*, *Oliva*, *Marginella*, etc., forming the rachiglossate arrangement represented by the formulas —, 1, —, or 1, 1, 1. In *Terebra*, *Conus*, *Pleurotoma* (Fig. 137, *C*), and allied genera the median tooth is absent, and the single admedian tooth on either side peculiarly long, forming the toxiglossate arrangement with a formula 1, 0, 1; and finally certain forms, such as *Ianthina*, *Scalaria* (Fig. 137, *D*), *Solarium*, etc., have a ptenoglossate arrangement in which the median is wanting but in which there are a large number of admedians, *x*, 0, *x*.

The suborder is relatively very rich in species, and consequently considerable variety of form is found. The majority are marine, but a few are fresh-water or even terrestrial in habitat. In these latter adaptations to their mode of life are found in modifications of the respiratory processes. In *Ampullaria* the single branchia persists, but in addition a comparatively capacious "lung cavity" is formed by a fold of the mantle, its walls being richly supplied with blood-vessels and its cavity being in communication with the exterior, so that air can be taken into and expelled from it. The species of this genus live partly in fresh water and partly are terrestrial, but in other forms, such as *Cyclostoma*, which are purely terrestrial, the branchia has entirely aborted, respiration being aerial and performed by the highly vascular wall of the mantle-cavity.

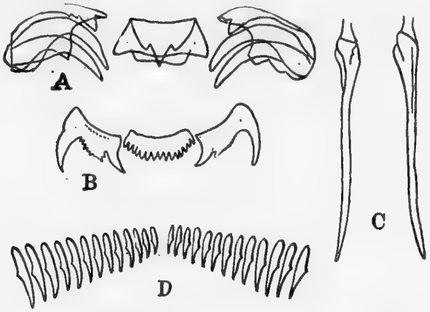


FIG. 137.—*A*, DENTITION OF *Natica*; *B*, OF *Nassa*; *C*, OF *Pleurotoma*; *D*, OF *Scalaria* (from BRONN).

The majority of the marine Monotocardia have a creeping habit, but a number are pelagic and form a group presenting many adaptive peculiarities which obtained for it the dignity of an order in older classifications. The members of this group, **HETEROPODA**, are more or less transparent animals, some of which, with this exception, present few differences from the other Monotocardia, while others are extensively modified. The genus *Atalanta* possesses a large transparent shell within which the animal can be completely retracted. The foot is no longer adapted for creeping, but is differentiated into a laterally flattened keel-like pro- and mesopodium which bears a sucker on its posterior surface, and a metapodium provided with an operculum. In *Carinaria* (Fig. 138) the visceral hump is reduced to a comparatively small mass upon the dorsal surface of the elongated body and is enclosed in a transparent shell shaped like a liberty-cap. The pro- and mesopodium have the form of a plate hanging down from about the middle of the under-surface of the body, and the metapodium is directed backwards, forming in reality the posterior portion of the body. The same relationships of the foot are found in *Pterotrachea*, which presents the extreme of modification found in this group; in this form the visceral hump is still more reduced than in *Carinaria*, forming only a small oval mass imbedded in the dorsal surface of the body and being destitute of any shell. Considering these two forms,

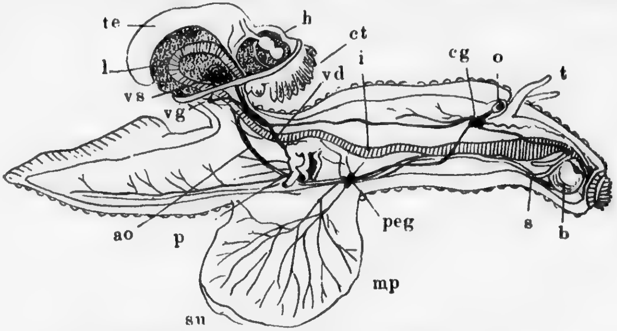


FIG. 138.—STRUCTURE OF *Carinaria mediterranea* (after OWEN).

ao = aorta.
b = buccal mass.
cg = cerebral ganglion.
ct = ctenidium.
h = heart.
i = intestine.
l = liver.
mp = mesopodium.
o = eye.
p = penis.
peg = pedal ganglion.
s = salivary gland.
su = sucker.
te = testis.
vd = vas deferens.
vg = visceral ganglion.
vs = seminal vesicle.

Pterotrachea and *Carinaria*, by themselves, the formation of a separate order for their reception would perhaps be justifiable, but *Atalanta* shows their close relationships with the Prosobranchia and indicates their true position as Monotocardia.

2. Order **Opisthobranchia.**

The Opisthobranchs are exclusively marine forms, presenting numerous modifications of shape and structure, but all agreeing in certain important particulars. The rotation of the mantle-cavity has not proceeded quite so far as in the Prosobranchs, the cavity and its organs lying upon the right side of the body, but at the same time the abortion of the organs of the primitively left side of the body has occurred. Thus in those forms which possess respiratory organs homologous with the branchiæ of the Prosobranchs, but one (that of the right side) is present, and with this character is associated the occurrence in the heart of but a single auricle, which lies behind the ventricle. Only one nephridium occurs, and a distinction from the Monotocardiate Prosobranchs is found in the fact that the branchia when present lies as indicated by the position of the auricle, behind the heart—the name bestowed upon the order being suggested by this peculiarity.

A more important distinguishing character perhaps is, however, to be found in the arrangement of the nerve-cords. A well-marked tendency towards an aggregation of the various ganglia to a complex mass lying behind the pharynx may be considered a characteristic of the Opisthobranchs. One or both parietal ganglia may disappear, and in some cases where there is a marked concentration of the ganglia the visceral ganglion may also be unrepresented, though usually from one to three such ganglia may be distinguished. In the figure of the nervous system of *Fiona* (Fig. 139) the concentration of the ganglia is well marked, but a decided asymmetry is made evident in some forms by the existence of a single parietal ganglion and of three visceral ganglia. In *Fiona*, however, the ganglionic concentration has been carried still farther, and at the same time by the suppression of the parietal ganglion as a distinct mass an apparent symmetry has resulted. Another notable feature is the usual absence of any apparent crossing of the nerve-cords. This condition, however, is probably due to the concentration of the ganglia, whereby the chiastoneurism is obscured, one of the most primitive of recent Opisthobranchs, *Actæon*, presenting well-marked chiastoneurism, associated with a somewhat discrete arrangement of the ganglia.

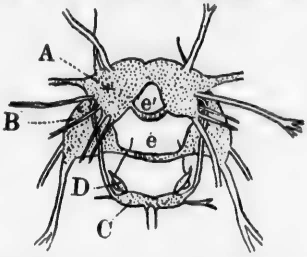


FIG. 139.—NERVOUS SYSTEM OF *Fiona atlantica* (after BERGH from GEGENBAUR).

A = cerebro-pleuro-visceral ganglion.
B = pedal ganglion.
C = buccal ganglion.
D = gastro-œsophageal ganglion.
e = pedal commissure.
e' = visceral commissure.

With regard to many other features of their anatomy considerable variations are to be found. Thus in some forms a well-developed spirally-coiled visceral hump is developed, while in others it loses its spiral arrangement, and in others again is elongated in the direction of the foot and can hardly be said to exist. So, too, with the occurrence of the shell, mantle, and branchiæ; all are well developed in some forms, but entirely absent in others. These peculiarities will be more conveniently referred to in connection with the various groups, and it is only necessary here to refer to another feature in addition to those already given, which is common to all the members of the order—i.e., the hermaphroditic character of the reproductive gland.

This forms part of the visceral mass and is usually composed of numerous lobes, these again being divided into secondary lobes or acini, the lining epithelium of which give rise to both ova and spermatozoa. In some forms, such as *Bulla* and *Aplysia*, both elements are formed in all the acini; but in others, such as *Doris*, *Janus*, Pteropoda, etc., the epithelium of the terminal acini gives rise to ova only; the epithelium of the lobes, i.e., the central portions of the gland, producing spermatozoa. Whether or not, however, there be such a separation of the epithelium into male and female areas, the reproductive elements make their way into a common *hermaphrodite duct*, which presents variations of structure in different forms and receives the secretion of certain accessory glands. In its simplest form, as seen for instance in *Aplysia*, the duct runs forward, pursuing a somewhat tortuous course and becomes surrounded by an *albuminiparous gland*, from which it receives a viscid secretion, within which the ova become imbedded just in front of the point where the gland opens into the duct. The latter has attached to it a pouch-like structure, the *vesicula seminalis*, and is continued on as a somewhat wider tube to open to the exterior at the genital pore situated on the right side of the body, shortly before reaching the pore, however, receiving a duct from a globular sac, the *spermatheca*. From the anterior edge of the pore a groove, the seminal groove, extends along the right side of the body to the neck region, where it ends in a muscular evertible penis, situated near the anterior right tentacle. It seems probable that the spermatozoa mature before the ova, and passing to the vesicula are stored up there. During copulation the seminal fluid is transferred through the penis to the spermatheca of another individual (perhaps the transference is a mutual interchange), and when later the ova pass along the duct they are impregnated by the spermatozoa so stored away, a cross-fertilization being thus brought about.

This arrangement of the reproductive duct is found in the more primitive Opisthobranchs, i.e., in those in which the mantle-lobe still persists, and in the group *Pteropoda*; in the more highly-modified forms, such as *Doris*, *Æolis*, etc., and, among the more simple forms, in *Pleurobranchæa* the hermaphrodite duct divides into an *oviduct* and a *vas deferens*. The former after receiving the spermathecal duct opens into a genital atrium, with which communicate also the albuminiparous gland and a *nidamental gland*, which manufactures the outer shell-like investment of the ova. The vas deferens, after a more or less tortuous course, enters the muscular saclike penis-sheath which communicates with the genital atrium; the enlarged termination of the vas, the penis, being thus capable of eversion through the pore by which the atrium communicates with the exterior. This condition seems to be a secondary modification of one in which the oviduct and vas deferens open independently at widely separated points—a condition which is represented by a few Opisthobranchs.

1. Suborder *Tectibranchia.*

The Tectibranchiates are those Opisthobranchs which present the smallest amount of modification from what has been considered the typical Gasteropod structure. A more or less developed mantle-fold is usually present, sometimes sufficiently voluminous to cover in the single branchia which persists (*Bulla*), but frequently represented only by a slight fold, which leaves the branchia exposed (*Aplysia*, *Gasteropteron*). A shell is very generally present, sometimes well developed (*Bulla*), but in other cases reduced to a plate-like structure enclosed within the mantle which has been reflected over it and the lips of the reflected portion meeting and fusing (*Aplysia*, *Pleurobranchus*). The visceral hump, however, is as a rule low and elongated in the direction of the long axis of the body instead of at right angles to it, as in the majority of Prosobranchs. In many members of the group the foot possesses a broad creeping surface, but its margins are prolonged into broad thin wings, the *parapodia*, which may be bent upwards, as in *Aplysia*, so as almost to enclose the body.

The Tectibranchiates are divisible into two groups according to their habits, in accordance with which the form of the foot and especially of the parapodia is modified. Those forms which possess a broad flat sole to the foot have a creeping habit; but there are many forms which are pelagic in habit and present many modifications of structure in adaptation to this mode of life, and were consequently classified at one time as a distinct order, the PTEROPODA, and consequently call for special mention. One of the most characteristic features of this group is the foot, which is limited to the anterior portion of the body and consists of a small median portion and two lateral wing-like parapodia arising from the sides of the median portion, and by the rapid flapping of which the animals are propelled through the water. In their general form much diversity is observable. In accordance with their pelagic habits the majority are more or less transparent; and some, the *Gymnosomata*, e.g. *Pneumoderma*, *Clione*, etc., are entirely destitute of a shell, mantle, and, except in *Pneumoderma* and its allies, of a branchia. Others, the *Thecosomata*, possess these structures, however—the shell in *Limacina* being spirally coiled, the mantle-cavity situated in front of the visceral hump being without a branchia; in *Styliola* the shell is not coiled, but is cone-shaped and bilaterally symmetrical, the mantle-cavity containing a gill; while in *Cymbuliopsis* the original shell is replaced by a cartilaginous case formed by the subepidermal tissues of the mantle, and the voluminous mantle-cavity contains no gill. The head of the Gymnosomata carries a non-retractile proboscis, at the extremity of which is situated the mouth, and it may furthermore bear in addition to the tentacles usually present peculiar tentacle-like processes, sometimes provided with suckers and perhaps

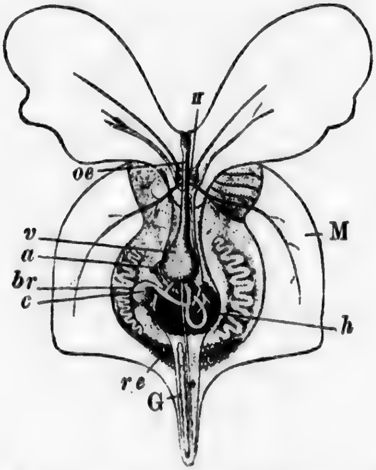


Fig. 140.—*Hyalea complanata* (after Gegenbaur, from Hertwig).

a = anus.
br = branchiæ.
c = heart.
G = reproductive organs.
h = digestive gland.
m = mantle.
oe = œsophagus.
re = nephridia.
v = stomach.
II = pedal ganglion.

modifications of portions of the foot, being innervated from the pedal ganglia. In these forms also fringed or simple processes of the posterior portion of the body occur which serve as respiratory organs, though they are not homologous with the true branchia which in *Pneumoderma* coexist with them.

2. Suborder *Nudibranchia.*

In the Nudibranchs the visceral hump has undergone elongation parallel with the long axis of the foot, from which it is not distinctly marked off, and an apparent bilateral symmetry is manifested by the body. This condition, however, is evidently entirely secondary, as is shown by the structure of the heart and nephridium, in which the usual asymmetry is well marked. There is no shell, mantle, or ctenidia. Adaptive branchiæ are, however, frequently developed, as in *Pleurophyllidia*, where they form a series of folds which lie in a groove at the side of the body and recall somewhat the arrangement in the Chitonidæ, or in *Doris*, where they surround the anus, which has a dorsal position, and form a circle of pinnate processes. In the pelagic *Phyllirhoë* and in the creeping *Limapontia*, however, there is no trace of respiratory organs. Many forms (Fig. 141), such as *Æolis*, *Facellina*, and their allies, bear upon the dorsal surface of the body numbers of finger-like processes usually arranged in bunches, and frequently brightly colored. These *cerata* frequently enclose branches from the intestine which correspond to the digestive gland of other forms, and bear at their extremities a sac in which are developed nematocysts. These organs are usually richly provided with blood-vessels, and are probably respiratory in function, though the presence of nematocysts renders it probable that they are also protective—an idea which is confirmed by their

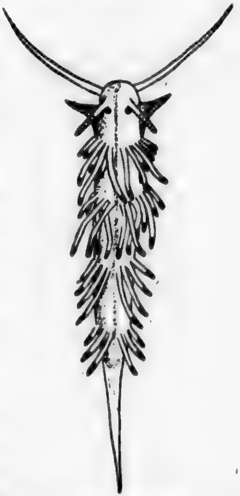


FIG. 141. — NUDIBRANCHIATE OPISTHOBRANCH (*Æolid*).

usually brilliant coloration. The foot in the pelagic *Phyllirhoë* has entirely disappeared, but is usually elongated and provided with a broad flat surface, in accordance with the creeping habits of the Nudibranchs. Parapodial folds, such as occur in the Tectibranchs, are never developed.

3. Order **Pulmonata.**

The Pulmonates differ from all the other groups of Gasteropods in that they are, with the exception of a single genus, *Onchidium*, either terrestrial or aquatic; and in adaptation to this assumed habit certain well-defined changes have occurred. In some genera, more especially the aquatic forms, such as *Limnæa*, *Physa*, and *Planorbis*, the visceral hump has its typical Gasteropod development, and is spirally coiled; but in many terrestrial forms, such as *Limax* (Fig. 142, *A*), *Arion*, and *Vaginula*, it is low and elongated parallel to the long axis of the foot with which it is fused. The mantle is in all forms well developed, but presents the peculiarity that it is fused by its edges to the body-wall except at one point upon the right side, where an opening is left by which the otherwise completely-closed mantle-cavity communicates with the exterior and through which air may be taken into the cavity. The position of the mantle-cavity, when not interfered with by secondary changes, is upon the right side of the body and somewhat in front of the visceral hump when this is present. A spirally-coiled shell is present in all forms in which the visceral hump is well developed, as in *Limnæa*, *Physa*, *Helix* (Fig. 142, *B*), and *Planorbis*, but in the elongated terrestrial forms a rudimentation of the shell accompanies the diminution of the visceral hump. Thus in *Daudebardia*, in which only a slight trace of the hump persists, the shell has become

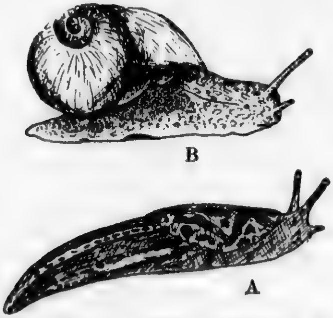


FIG. 142.—*A*, *Limax maximus*; *B*, *Helix* (after HOWES).

quite small, though still showing plainly a spiral form; but in *Limax* it is represented only by a partially calcified plate, imbedded in the roof of the mantle-cavity by the closure over it of a fold of the mantle. In *Arion* only a few isolated particles of carbonate of lime persist, while in *Vaginula* and *Onchidium* all trace of it has disappeared.

A marked characteristic of the Pulmonata is found in the character of their respiratory organ. A ctenidium is entirely wanting, the only trace of its existence being the occurrence in some of the aquatic forms (*Limnæa*, *Physa*, etc.), of an osphradium near the mantle-pore. Its place is taken by the roof of the mantle-cavity, which receives a rich vascular network and functions as a lung, the mantle-cavity containing air which can be renewed through the mantle-pore. The heart is situated far back in the mantle-cavity, its auricle lying in front of the ventricle and receiving the blood from the more anteriorly-situated lung, so that the relation of the respiratory organ to the heart is the same as obtains in the Prosobranchs. In the immediate neighborhood of the heart lies the single nephridium, opening into the mantle-cavity or else into the terminal portion of the rectum (*Helix*), this structure opening on the right side of the body in close proximity to the mantle-pore.

Like the Opisthobranchs, the Pulmonates present an orthoneurous arrangement of the pleuro-visceral connectives; but here also the absence of a crossing of the nerve-cords is probably a secondary condition, depending on the concentration of the various ganglia to a compact mass, since in a South American form, *Chilina*, in which the concentration of the ganglia has not progressed as far as usual, a chiastoneurism is apparent.

Special visual organs are invariably present with the structure which has already been described. In some forms they are situated, as in the Prosobranchs, at the bases of the tentacles; while in others they are found at the tips of these structures—the Pulmonates being divisible, according to the situation of the eyes, into the *Basommatophora*, including such forms as *Limnæa*, *Physa*, *Planorbis*, and in general the aquatic forms, and the *Stylommatophora*, which includes the terrestrial forms, and *Onchidium*.

This last genus in addition to the usual eyes borne upon the tentacles is in some species further provided with a number of eyes situated upon the back and differing from the typical eye in the arrangement of the retinal cells. As has been seen, the optic nerve in typical eyes on entering the eye spreads out in a layer to form the retina, the terminal optic cells being situated on that surface of the retina which is turned towards the light. The dorsal eyes of *Onchidium*, however, present a somewhat different arrangement, the cells in which the nerve-fibres terminate having their distal ends turned away from the light, which to affect them must pass through the layer of nerve-fibres formed by the spreading out of the optic nerve. Compared with the retinæ of typical eyes, those of the dorsal eyes of *Onchidium* are inverted and have assumed an arrangement exceedingly rare in Invertebrates, but typical for the lateral eyes of the Vertebrata.

Otocysts are always present, and the tentacles borne by the head are probably tactile in function. In the Stylommatophorous Pulmonates there are in some cases (*Helix*) two pairs of such tentacles, the eyes being situated upon the posterior pair, both pairs furthermore being capable of being invaginated for protection into the body-cavity, a peculiarity not presented by the tentacles of the Basommatophora. As stated above, the osphradium is represented in certain aquatic forms, but in the Stylommatophora it has disappeared with the suppression of the ctenidium.

The Pulmonata are hermaphrodite, the epithelium of the reproductive gland (Fig. 143, *hg*) differentiating into both spermatozoa and ova, there being no localization of the formation of either one or the other in a special portion of the gland, as happens in some Opisthobranchs. In the Basommatophora and certain terrestrial Pulmonates, such as *Vaginula* and *Onchidium*, the common duct (*hd*) for the spermatozoa and ova divides and passes to the exterior by two distinct and separate apertures. Thus in *Limnæa* the hermaphrodite duct shortly after leaving the gland divides, and into one of the branches immediately after the division there opens a well-developed albuminiparous gland (*al*), and it then becomes somewhat folded, forming what is termed the uterus (*ut*). Beyond this structure the duct, now known as the oviduct (*od*), receives the duct of a nidamental gland and dilates into a large pyriform structure, which tapers somewhat to form a vagina opening to the exterior and receives a duct from the receptaculum seminis. The vas deferens (*vd*) shortly after its separation from the hermaphrodite duct dilates into a glandular structure, the prostate gland, from which the narrow duct passes onward to terminate in an enlarged penis-sheath (*pe*) which contains the muscular protrusible penis and opens to the exterior quite independent of the opening of the vagina.

In the majority of the Stylommatophora (Fig. 143), however, the two ducts open into a common atrium so that only one genital orifice occurs, as in some of the Opisthobranchs (see p. 312). Otherwise the arrangement is similar to what has been described for the Basommatophora, except that in some forms, as *Helix*, one or two additional accessory structures are added. Thus the atrium has communicating with it a sac which contains a sharp calcareous rod, the "dart," which serves as a stimulus during copulation, being plunged into the body of the other party to the act; and again just at the point where the vas deferens opens into the penis it has communicating with it an elongated tubular structure, the "flagellum," which perhaps furnishes the material of which the capsule of the spermatophores is composed.

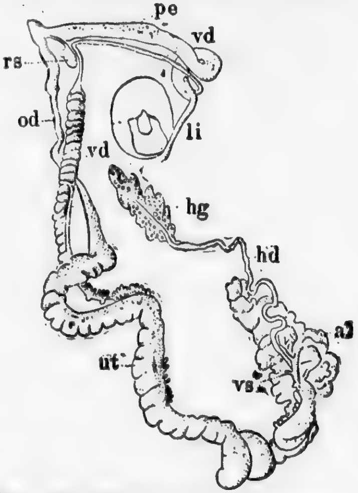


FIG. 143.—**REPRODUCTIVE ORGANS OF** *Limax maximus* (after SIMROTH).

al = albuminiparous gland.
hd = hermaphrodite duct.
hg = hermaphrodite gland.
li = ligament.
od = oviduct.
pe = penis-sheath.
rs = receptaculum seminis.
ut = uterus.
vd = vas deferens.
vs = vesicula seminalis.

Development and Affinities of the Gasteropods.—The development of the Gasteropods is made interesting on account of the occurrence in the majority of forms of a larva known as the *Veliger* (Fig. 144) which presents many interesting affinities to the Annelid Trochophore. In the early stages of development the embryo is strictly bilateral, with the mouth and anus at the extremities of the longitudinal axis. Upon the dorsal surface posteriorly is a depression lined with columnar cells which secrete the larval shell (*Sh*), and in front of this is an area enclosed by two rows of cells bearing stout cilia and forming the velum (*V*). This band of cilia is præoral (*Pro*) in position, and in addition to it a second band of smaller cilia is to be found which passes ventrally to the mouth and constitutes a postoral band (*Poo*), the groove between it and the præoral band being occupied by the adoral cilia. On the ventral surface is found a prominence which represents the foot.

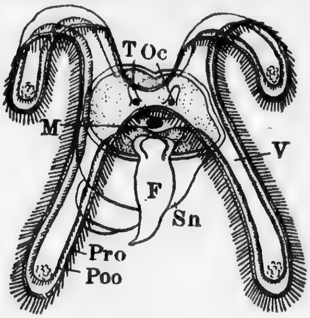


FIG. 144.—VELIGER LARVA.

F = foot.
M = mouth.
Oc = eye.
Poo = postoral band of cilia.
Pro = præoral band of cilia.
Sh = shell.
T = tentacle.
V = velum.

In later stages the lateral edges of the velum are drawn out so as to form a broad lobe, sometimes divided into two arms, projecting on each side of the head; the præoral and postoral bands of cilia extending round the margin of the fold, not, however, completely enclosing the velar area, but remaining open on the dorsal surface. The shell area increases markedly in size, the shell becoming spirally coiled, the visceral hump which develops in the shell area likewise assuming the coiled form. At the margins of the shell area a fold appears, the rudiment of the mantle, which gradually increases in size as the shell area extends, and at the same time the anus becomes rotated forwards from its original terminal position along the right side of the body to a greater or less extent. As these changes progress, the embryo gradually approaches more and more to the adult form, differing from it mainly in the existence of the velum, by means of which it leads a free-swimming pelagic existence, assuming the adult habit only after a further growth which is accompanied by a reduction of the velum.

Such a Veliger larva occurs in the life-history of the majority of the Gasteropoda, though, as might be expected, it undergoes certain modifications more especially in terrestrial forms, though even in these there are ample indications of its existence. Indeed the Veliger is so frequent in its occurrence that the conclusion is almost unavoidable that it has an ancestral significance and represents in a more or less modified condition a primitive form from which the Mollusca have descended. A comparison of the Veliger with the Annelid Trochophore brings out, as already mentioned, numerous similarities. These are especially noticeable in the arrangement of the ciliary bands, which resemble those of the Trochophore part for part, even to the dorsal break in their continuity. It is difficult to believe that such marked similarities should have been acquired independently in the larvæ of two different groups of animals and have become so characteristic, a difficulty rendered all the greater by the occurrence of other points of similarity, such as the development of the mesoderm, in some forms at least, from a pair of mesoblasts situated at the posterior extremity of the blastocœl; the existence of a thickening of the ectoderm in the centre of the velar area in some forms, corresponding to the apical plate of the Trocophore; and the occurrence of a larval excretory organ or nephridium in some Veligers which may be compared to the larval nephridium or head-kidney of the Trochophore. The probable significance of this larval form will be more suitably discussed at the conclusion of this chapter; it remains to be said here regarding it that the occurrence among the Pteropods of larvæ with several bands of cilia surrounding the visceral hump is probably to be explained as a secondary adaptation, just as the mesotrochal Annelid larvæ are probably secondary modifications of a Trochophore.

As regards the relationships of the various groups of Gasteropods among themselves, there is little doubt but that the Diotocardiate Prosobranchs are, on the whole, the most primitive of all the groups and stand nearest to the Amphineura, and from them the Monotocardia have developed. The Opisthobranchs and Pulmonates are apparently closely related, the latter group having been derived from Tectibranchiate ancestors somewhat more generalized probably than any Opisthobranch now living. The orthoneurous character of the nervous system and the structure of the reproductive system in the two groups indicates their affinity, and it seems probable that the Pulmonates are to be regarded as Opisthobranchs which have accommodated themselves at first to an amphibious life, somewhat similar to that now led by *Onchidium*, and later to one purely terrestrial, at the same time differentiating an organ for aerial respiration. Such an origin would imply that the aquatic species have secondarily taken to fresh water as a habitat, having originally been terrestrial, an idea which on *a priori* grounds seems improbable; but there seems to be no good reason, if the aquatic forms are derived directly from marine ancestors, why their ctenidia should have become replaced by a lung, since in the aquatic Prosobranch *Paludina* the ctenidium is still retained. On the other hand, it may be again mentioned that the terrestrial Prosobranchs such as *Cyclostoma*, *Acicula*, etc., have lost their ctenidium and resemble a Pulmonate in their mode of respiration.

III. CLASS **SCAPHOPODA.**

The class Scaphopoda contains a small number of closely-related genera of marine Mollusca, *Dentalium*, *Siphonodentalium*, *Cadulus*, etc., living imbedded in the sand in depths of from 10 to 100 fathoms and possessing but slight powers of locomotion. They resemble the Gasteropoda in possessing a visceral hump which is relatively enormously elongated but does not undergo a spiral twisting, nor has it fallen over to the right or left side of the body. Consequently the Scaphopods are bilaterally symmetrical and stand in marked contrast in this respect to the Gasteropods.

The mantle-folds are two in number, arising from the anterior surface of the visceral hump and extending around the body so as to completely enclose it, meeting posteriorly and fusing together, except for a short extent, dorsally and ventrally, and forming thus a tube to the anterior wall of which the body is as it were attached. This tube is open at either end, the ventral opening being somewhat larger than the dorsal one, and the whole is enclosed within a tubular shell (Fig. 145, *sh*) whose shape corresponds essentially to that of the mantle. From the ventral opening the foot (*f*) projects to a greater or less extent, being in *Dentalium* a cylindrical structure, terminating in a conical process provided with two lateral lobes.

The mouth (*m*) is situated at the extremity of a cylindrical proboscis (not to be confounded with the protrusible proboscis of a Gasteropod) and is surrounded by a number of leaflike tentacles, while at the base of the snout there is upon each side a bunch of long filamentous tentacles (*t*) capable of being protruded from the mouth of the shell and of being withdrawn within it. Each tentacle terminates in a spoon-shaped structure whose concave surface is furnished with ciliated cells and also towards the margin with unicellular glands. These structures have been supposed to represent the ctenidia of the other Mollusca, but this view cannot, in the present condition of our information concerning their structure and development, be accepted without reservation. The mouth opens into a short œsophagus provided with a single chitinous jaw-tooth apparently formed by a fusion of two chitinous masses, and behind this there is a pharynx provided with a radula and opening posteriorly into the somewhat U-shaped more or less convoluted intestine (*i*) which terminates in the anus (*a*) lying in the mid-ventral line behind the foot. Into the intestine at the turn of the U there open the ducts of the digestive gland (*l*), and into the posterior portion of the intestine, the rectum, there open in *Dentalium* several ducts from a rectal gland which surrounds this portion of the digestive tract and whose significance is quite obscure.

The nervous system presents the majority of the ganglia characteristic of the Gasteropoda, and the pleuro-visceral connectives do not cross one another. The cerebral ganglia (*ce*) lie at the base of the proboscis anterior to the œsophagus and have closely associated with them the pleural ganglia, the cerebro-pedal and pleuro-pedal connectives fusing with one another to pass downwards and forwards to the pedal ganglion (*pe*) situated in the foot. Posteriorly in the vicinity of the rectum lie the two visceral ganglia (*vi*) from which long

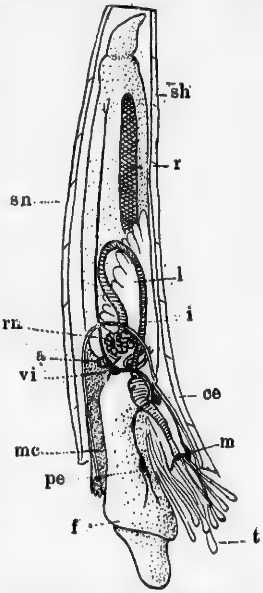


Fig. 145. — **Structure of** *Dentalium* (after Leuckart).

a = anus.
ce = cerebral ganglion.
f = foot.
i = intestine.
l = liver.
m = mouth.
mc = mantle-cavity.
pe = pedal ganglion.
r = reproductive organ.
rn = right nephridium.
sh = shell.
t = tentacle.
vi = visceral ganglion.

nerves pass dorsally, but no special parietal ganglia occur. Two pairs of buccal ganglia are also present. Otocysts are present imbedded in the foot in the neighborhood of the pedal ganglia, but no other special organs of sense, unless the bunches of tentacles be considered such, occur.

No special respiratory organs are developed, the mantle probably subserving the respiratory function. The heart, a simple invagination of the wall of the pericardial cavity, lies in the posterior region of the body, on the dorsal surface of the intestine. It possesses no auricle, but receives the blood through small slits in its walls. There are no special blood-vessels, but the blood circulates through a series of sinuses traversing the body in various directions.

A pair of nephridia occurs in the posterior region of the body, opening to the exterior by a pore on either side of the anus, but a communication with the pericardial cavity is said to be wanting. However this may be, the right nephridium (*rn*) serves for the exit of the reproductive elements, though the exact method by which these latter make their way into the duct is unknown. Between each nephridial pore and the anus there is a pore which seems to be the opening of a short tube which communicates directly with the schizocœlic sinus surrounding the terminal portion of the intestine and places it in communication with the surrounding water, a peculiar arrangement which recalls the dorsal pores of the oligochætous Annelids. The Scaphopods are bisexual, and the reproductive organs, ovaries or testes, are single, consisting of long completely closed sacs with lateral diverticula, lying along the posterior wall of the visceral hump. As already stated, the reproductive elements after the rupture of the wall of the reproductive gland make their way to the exterior through the right nephridium.

Development and Affinities of the Scaphopoda.—The larva of *Dentalium*, though presenting considerable resemblance to the Trochophore, differs from it nevertheless in several points of detail. It possesses a distinct apical tuft of cilia and the prototroch is present, though represented by three or more circles of cilia-bearing cells. The mantle-folds develop at a relatively early stage as two lateral folds, quite separate along the ventral line, the fusion characteristic of the adult only appearing later. It is this early development of the mantle-lobes and the multiplication of the prototroch bands which obscure the Trochophore characters, a still earlier larva presenting greater similarities to the annelid larva.

By the earlier writers the Scaphophods were considered more closely related to the Pelecypoda than to the other Molluscan groups, this relationship being indicated more especially by the symmetrical form, the apparent lateral arrangement of the mantle-folds and the absence of eyes. On the other hand, there are a large number of differences between the members of the two groups, as for instance the univalve character of the shell, and especially the occurrence of a radula and jaw. This latter feature suggests the Gasteropods, and it seems most probable that it is to this group that the Scaphopods should be considered as related. They must, however, be referred to the more primitive Gasteropods, those in which the rotation of the mantle-chamber had not occurred. An elongation of the dorsal hump of a *Fissurella*-like ancestor unaccompanied by a twisting to one side, as represented in Fig. 146, would bring about a condition from which it does not seem a great step to reach the Scaphopods.

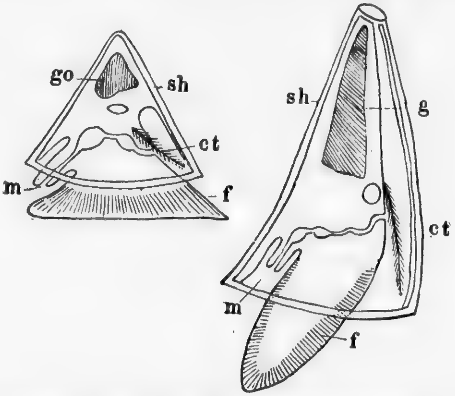


Fig. 146.—Diagrams to show the Origin of the Scaphopods from a *Fissurella*-like Ancestor (after Plate).

ct = ctenidium.
go = reproductive organ.
f = foot.
m = mouth.
sh = shell.

Among recent Gasteropods it is with the Diotocardiates that the Scaphopods seem to be most affiliated, and, as we shall later see, it is from the primitive members of this order that the Pelecypods have probably been derived, and thus any similarities which may exist between the Scaphopods and Pelecypods is readily explicable on the basis of a similar ancestry, both groups being derived from Prosobranch-like forms. The absence of a larva corresponding closely to the Gasteropod Veliger would seem to oppose such a view, but it must be remembered that the Veliger is characteristic only of the more highly-differentiated Prosobranchs—such forms as *Patella*, for instance, having a larva destitute of some of the more characteristic Veliger features and more closely resembling the Annelid Trochophore and the Scaphopod larva.

IV. CLASS **PELECYPODA.**

The class Pelecypoda, also known as the *Lamellibranchia*, contains a number of fresh-water genera, though the majority are marine, and all its members retain the primitive bilateral symmetry of form, no visceral hump being developed. The body is more or less laterally compressed and two large mantle-folds (Fig. 149, *m*) are developed, arising one on each side a short distance ventrad of the dorsal mid-line and extending downward so as to meet below. They thus enclose a wide space, the mantle-cavity, between their inner surfaces and the body-wall, within which lie the ctenidia (Fig. 148, *ct*) and the foot (*p*). Upon the mantle-edge in many forms tentacles, papillæ, glands, and eyes are developed, and in many cases the edges of the two lobes may fuse more or less completely, openings being, however, left for the entrance and exit of water into the mantle-cavity, and also for the protrusion of the foot. All gradations of fusion are represented: thus in *Nucula*, *Ostrea*, etc., there is no fusion whatever; in *Unio* (Fig. 149) and other forms the posterior edges of the mantle-folds are modified, so that while the edges of the folds are in contact throughout the greater portion of their extent two openings are left, through the uppermost of which, the exhalent opening (*eo*), water carrying with it the excreta and the reproductive elements finds an exit, while through the lower one, the inhalent opening (*io*), fresh water passes in; in the next gradation the point of separation between these two openings, which in *Unio* was simply formed by the contact of the mantle-edges, becomes permanent by the fusion of these latter parts, and a further stage, seen in *Venus* for example, is formed by the fusion of the mantle-edges ventral to the branchial opening, a fusion which may extend forward a considerable distance. In this last condition there are three openings which place the mantle-cavity in communication with the exterior, one anterior, through which the foot is protruded, and two posterior, the branchial and anal openings. The mantle around these latter frequently becomes prolonged so that two tubes, or siphons as they are termed, are formed, sometimes in contact with one another (*Pholas*), sometimes quite separate (*Venus*), sometimes capable of retraction within the shell, sometimes so large as to be incapable of retraction (*Mya*).

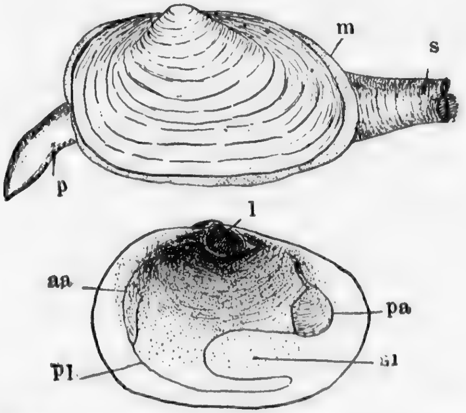


FIG. 147.—*A*, *Mya arenaria* with the siphons slightly expanded; *B*, inner surface of the right valve of the shell of *Mya*.

aa = impression of anterior adductor muscle.
l = ligament.
m = mantle edge.
p = foot.
pa = impression of posterior adductor muscle.
pl = pallial line.
s = siphon.
si = siphonal impression.

In conformity with the form of the mantle-lobes the shell consists of two similar portions or valves, lying on the sides of the body and united along the dorsal mid-line by a hinge. The hinge is formed by a ligament, as it is termed, which is really a portion of the shell substance, and consists of an external portion continuous with the epidermis of the shell and an internal elastic portion, frequently calcified to a certain extent, and continuous with the middle layer (prismatic layer) of the shell. When at rest the two valves of the shell are kept apart along the ventral line by the elasticity of the hinge-ligament, and it is only by the application of force that the two valves can be brought together, the ligament being then compressed. The hinge is frequently complicated by the development of tooth-like processes and corresponding sockets so that the two valves may be firmly locked together. Upon the inner surface of the valves are certain impressions produced by the softer parts and of considerable value in systematic conchology. A short distance from the margin of each valve and parallel to it is a distinct line, the pallial impression (Fig. 147, *pl*), produced by the attachment of the muscle-fibres which bind the mantle-lobes to the shell. In some forms, such as *Anodon*, this pallial line follows the shell margin throughout its entire course, but in those genera which possess well-developed and retractile siphons it is deeply incurved in the posterior portion of its course. Other markings of the shells are produced by the insertion into them of a number of muscles. The largest and most important of these are the adductor muscles of the shell (*aa*), large muscles passing from one valve to the other, by their contraction overcoming the elasticity of the hinge-ligament and closing the shell. In the majority of forms there are two such muscles, situated towards the anterior and posterior portion of the body, but not unfrequently, as in *Ostrea* and *Pecten*, but one, corresponding to the posterior adductor of other forms, is present. In the immediate vicinity of the adductor-impressions other smaller muscle-impressions are usually observable, produced by the protractor and retractor muscles of the foot and siphons.

Although in the Pelecypod shell the two valves are typically similar and symmetrical, yet in a number of cases a marked dissimilarity is found in their shape. Thus in *Ostrea* the valve upon which the animal rests, usually the left valve, is large and concave, while the other is smaller and flattened, and a similar relation is found in other forms which become temporarily fastened to rocks, etc. Occasionally additional calcareous plates are added to the usual shell, as in the boring mollusk *Pholas*, in which three accessory calcareous plates are developed on the dorsal surface of the body. In the Ship-worm, or *Teredo*, which bores extensively into timber and is in some cases exceedingly destructive, the true shell-valves are very small and situated at the anterior end of the body, and the mantle projects backwards far beyond them and secretes a thin calcareous tube which lines the interior of the passages excavated by the animal. A similar peculiarity is found in the *Aspergillum*. Here, too, the true shell-valves are exceedingly small and are united together by and imbedded in a calcareous tube secreted by the mantle, which projects far beyond the shell proper and is fused throughout the greater portion of its extent. The calcareous tube is open behind for the passage of the two siphons, but anteriorly is closed by a perforated plate, the margins of the perforations being sometimes prolonged into tubes which may branch dichotomously. The animal lives imbedded in the sand, the posterior extremity of the shell being directed upwards, and seems to have been derived from forms originally possessing a boring habit, such as is seen in *Teredo*.

The foot of the Pelecypoda is as a rule very simple. In the most primitive members of the group, such as *Nucula* (Fig. 151), it is a flat disk-like structure, recalling somewhat the foot of the Gasteropoda, but more usually it is a keel-shaped structure (Fig. 149, *p*). The modifications in shape which it undergoes are, however, numerous and it may even in some cases be almost absent, as in the Oyster (*Ostrea*), but special developments, such as epipodia, are never found in connection with it. A "byssus-gland" is a characteristic development of the Pelecypod foot, consisting of a cavity with usually greatly folded walls lying in the tissues of the foot and connected with the exterior by a canal opening on the sole of the foot. By the cells lining the cavity threads of a horny consistency are secreted by means of which the animal is enabled to fasten itself to stones, etc., or even in some cases, as *Mytilus*, to move about in the absence of a well-developed foot, throwing out byssus filaments, attaching them, and then drawing itself forward towards them.

The respiratory organs (Fig. 149, *br*) of the Pelecypoda consist of a pair of platelike structures situated on each side of the body, and being attached along their dorsal margins hang down between the mantle and the body-wall. Notwithstanding their platelike form they are modifications of the plumose ctenidium of the Gasteropods. If the typical bipinnate ctenidium be imagined to be directed parallel to the long axis of the body and the median axis to have fused with the body-wall, so that the two rows of pinnæ are bent down so as to lie parallel to one another, the simplest form of the Pelecypod ctenidium, such as occurs in *Nucula* (Fig. 151), will be obtained. In the majority of forms, however, the arrangement is much more complicated than this. Thus in *Mytilus* it will be found that the various pinnæ composing each plate are held together by a series of patches of strong cilia which interlock forming the "ciliated junctions," and furthermore the pinnæ are at their free ends bent abruptly upon themselves, those of the outer row outwards and those of the inner row inwards, so that each gill-plate is composed of two lamellæ (Fig. 148, *A*). This condition may be regarded as the next step in the modification, which is continued even further by the permanent union of the outer and inner limbs

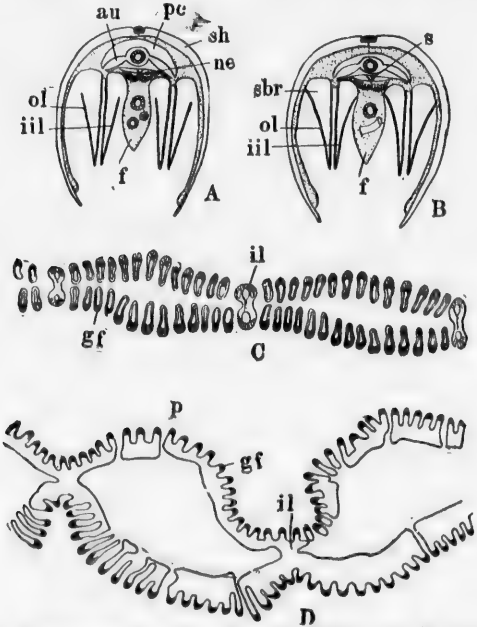


Fig. 148.—*A*, diagrammatic section through *Pecten*, and *B*, through *Anodon*; *C*, section through gill-lamella of *Pecten*, and *D*, of *Anodon*.

au = auricle.
f = foot.
gf = gill-filament.
iil = inner lamella of inner gill.
il = interlamellar junction.
ne = nephridium.
ol = outer lamella of outer gill.
pc = pericardial cavity.
p = pore.
s = blood-sinus.
sbr = suprabranchial chamber.
sh = shell.

of the pinnæ, or gill-filaments as they may be called, by hollow processes, the "interlamellar junctions" (Fig. 148, *C*, *il*). A still greater departure from the primitive condition is found, however, in the greater number of existing Pelecypods, consisting of a fusion of all the filaments of each lamella into a plate (Fig. 148, *D*), small openings (*p*) only being left here and there between adjacent filaments; furthermore the interlamellar junctions become very well developed, so that the two lamellæ of each gill become firmly united together to form a plate, containing in the interior a cavity, the interlamellar space.

In addition to these various modifications which lead to the formation of a true lamellate gill, the edge of the external lamella of the outer plate fuses with the inner surface of the mantle, and the internal lamella of the inner plate fuses similarly with the side of the foot (Fig. 148, *B*), and the mantle-cavity thus becomes divided into two chambers. Into the ventral chamber the inhalent siphon opens, and the water which enters by it passes through the openings left between the filaments and so reaches the interlamellar spaces which communicate above with the dorsal or suprabranchial chamber (*sbr*), whence it passes to the exterior through the exhalent siphon. In the region of the foot the suprabranchial chamber is of course divided into two portions, one of which lies on each side of the base of the foot, and each of these is again divided longitudinally into an inner and an outer portion by the line attachment of the gills to what may be considered the roof of the mantle-cavity. Behind the foot the inner cavities of the two sides unite and in some forms open ventrally into the mantle-cavity proper; in others, however, the inner lamellæ of the inner gill-plates fuse with one another along the middle line so that a distinct partition, formed by the gills, separates the suprabranchial chamber from the ventral mantle-chamber throughout its entire length In a few forms, such as *Cuspidaria*, the gills become reduced to simple muscular partitions perforated by pores and separating the two chambers, practically all indication of the original ctenidium characters having disappeared.

The muscular system of the Pelecypoda reaches a somewhat extensive development in connection with the presence of the bivalved shell. The mantle-folds are as a rule somewhat richly provided with muscle-fibres especially near the margin; and where siphons are developed some of the fibres are specialized into retractors for these organs. For the closure of the shell-valves, however, more extensive muscular bands are present which seem, like the siphonal retractors, to be specialized portions of the mantle musculature. Of these shell-adductors there may be one, as in *Ostrea and Pecten*, or two, as in *Anodon* (Fig. 149, *aa* and *pa*), which pass transversely across the body from one shell-valve to the other, in the form of stout compact muscular bands. In connection with the foot special bands are also developed which function as protractors (*pp*), retractors (*rp*), and elevators arranged in pairs and extending from the inner surfaces of the shell-valves to spread out below in the foot. These various bundles seem to correspond to the spindle-muscle of the Gasteropods.

The cœlom presents an arrangement similar to that of other Mollusca, both schizocœlic and enterocœlic portions being distinguishable. To the former portion belong the numerous lacunar spaces which traverse the body and mantle-folds, and to the latter the pericardial cavity (Fig. 149, *p*) and the cavity of the reproductive glands. The blood-vascular system consists of a heart provided with two lateral auricles and lying in the pericardium. In the majority of forms the ventricle (*v*) seems to be traversed by the terminal portion of the digestive tract, a condition produced by its having folded itself longitudinally around the rectum, and which recalls what occurs in certain Diotocardiate Gasteropods (see p. 305). This arrangement does not, however, obtain in all forms, some of the more primitive (*Nucula*, *Arca*) having the ventricle entirely dorsal to the intestine, as it is in the Amphineura, for example, while in a few others (*Ostrea*) it has assumed a secondary position ventral to the intestine. From both the anterior (*ao*) and posterior extremities of the ventricle arteries arise which, after branching a number of times, pour the blood into the schizocœlic lacunar system. Traversing this the venous blood is returned to a longitudinal sinus lying in the middle line of the body just below the pericardium (Fig.

148, *B*, *s*), whence the greater portion passes into the complicated network of the nephridia and thence to a blood-vessel, the branchial artery, running along the base of the gill of each side. After traversing the gill-filaments it becomes arterial and is returned to the branchial veins which run parallel to the branchial arteries and thence is returned to the auricles of the heart.

The digestive tract has a much simpler structure than in the majority of the Mollusca, lacking all trace of a radula and muscular pharynx. On each side of the mouth are two usually triangular plates, the so-called labial palps, the uppermost of which meet above the mouth forming a sort of upper lip, while the lower ones similarly form a lower lip. At the bottom of the space separating the two palps of each side is a groove which, starting at the sides of the mouth, runs backwards along the sides of the body to the gills. This groove serves for the conduction to the mouth of the particles of food brought into the mantle-cavity by the action of the cilia of the gills, the food of the Pelecypods consisting of diatoms and other minute organisms capable of being captured in this manner. The œsophagus opens into a stomach (Fig. 149, *s*) which receives by numerous openings the secretion of the usually voluminous digestive gland (*l*), the so-called liver, and passes posteriorly into the intestine (*i*), which, usually in several convolutions, lies imbedded in the tissues of the base of the foot. In the wall of the anterior portion of the intestine is a groove, frequently converted into a canal, which may open into the stomach by an independent opening; the epithelium of this groove or canal secretes a substance which forms a transparent glass-like rod lying in the canal and projecting into the lumen of the intestine. The function of this crystalline style, as it is termed, has been the subject of much speculation, the most plausible theory being that the secretion serves to surround sharp-edged particles of sand or similar substances, taken into the intestine with food, with a jelly-like coating which will prevent them from injuring the delicate walls of the intestine. Towards its posterior end the intestine bends upwards, i.e. dorsally, to a point in front of the heart and then passes directly backwards to terminate in the anus (*a*) which opens into the suprabranchial chamber (*sbr*) in the vicinity of the exhalent siphon. The relations of this rectum to the heart have already been noted (p. 332).

The nervous system of the Pelecypoda differs somewhat apparently from that of the Gasteropods, a smaller number

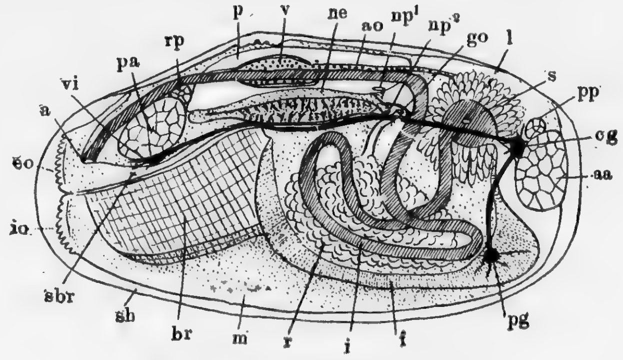


FIG. 149.—STRUCTURE OF *Anodon*.

a = anus.
aa = anterior adductor.
ao = aorta.
br = gill.
cg = cerebral ganglion.
eo = exhalent orifice of siphon.
f = foot.
go = genital orifice.
i = intestine.
io = inhalent orifice of siphon.
l = liver.
m = mantle.
ne = nephridium.
np^1 = nephridial opening into pericardial cavity.
np^2 = nephridial opening into suprabranchial chamber.
p = pericardial cavity.
pa = posterior adductor.
pg = pedal ganglion.
pp = protractor pedis.
r = reproductive organ.
rp = retractor pedis.
s = stomach.
sbr = suprabranchial chamber.
sh = shell.
v = ventricle.
vi = visceral ganglion.

of ganglia being discernible. Above the œsophagus a short distance behind the mouth is on either side a well-marked ganglion (Fig. 149, *cg*) connected with its fellow of the opposite side by a transverse commissure. In the more primitive forms (*Nucula*) two ganglia are found on either side, of which one evidently corresponds to the cerebral and the other to the pleural ganglion of the Gasteropods. Where, therefore, as in the majority of the Pelecypods, but a single ganglion occurs on each side, it is to be regarded as a cerebro-pleural ganglion. From each of these a pedal connective passes downwards into the foot to terminate in a paired pedal ganglion (*pg*), and a second strong connective passes backwards on each side of the base of the foot to terminate in a large ganglion (*vi*), situated below the rectal portion of the intestine and frequently in close proximity to the posterior adductor muscle, and which from its relations is evidently to be regarded as representing both the parietal and the visceral ganglia of the Gasteropods and hence may be termed the viscero-parietal ganglion.

The sense-organs are of essentially the same nature as in the Gasteropods. Tactile cells exist scattered over the surface of the body, and are especially numerous in certain localities, as upon the siphons when these are present. A pair of osphradia are also present situated above the viscero-parietal ganglion close to the insertion of the bases of the gill-plates into the side of the body; and imbedded in the tissues of the foot, usually in close proximity to the pedal ganglia, though innervated by the cerebro-pleural, are a pair of otocysts having the usual structure (see p. 283). In a number of forms paired elevations, evidently of a sensory nature, have been found in the neighborhood of the inner ends of the siphons, or on the sides of the body a little in front of the anus; the function of these is doubtful, though it has been suggested that they are olfactory.

Eyes are present in a number of forms and present various degrees of complexity. In some cases a perception of sudden variations in the intensity of light is present, as in the siphons of some forms, without any distinct optic sense-organs being developed. Sensory and pigment cells are present, however, and may be regarded as forming a diffuse optic organ. No eyes occur upon the head, nor are tentacles developed in any of the Pelecypods, but large numbers of eyes are developed upon the edge of the mantle of many forms, such as *Pecten* and *Spondylus*. These eyes may be simple depressions of the mantle-margin, the bottom of the depression being lined with pigmented and sensory cells, a cuticle of varying thickness covering this retinal surface. Another form of eye (Fig. 150) also occurs upon tentacular processes which presents an arrangement unusual for Invertebrates. The extremity of the process is occupied by a number of clear transparent cells which serve as a cornea (*co*) and which are continuous with a zone of pigmented cells (*pg*) analogous to an iris, and which pass gradually over into ordinary ectodermal cells. Upon the inner surface of the cornea is a mass of transparent cells constituting a lens (*l*), and below this lies the sensory portion of the eye. The optic nerve as it comes towards the eye branches;

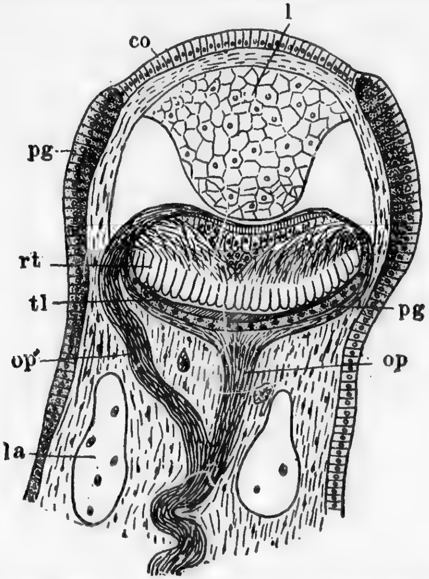


FIG. 150.—EYE OF *Pecten* (modified slightly from PATTEN).
co = cornea.
l = lens.
la = blood-lacuna.
op, *op'* = optic nerve.
pg = pigment-cells.
rt = retina.
tl = tapetum lucidum.

one branch (*op'*), passing to one side of the eye, bends inwards towards the axis of the eye between the retina-cells (*rt*) and the lens. The sensory portion of the eye consequently is inverted, the retina-cells being turned away from the light which must pass through the fibres of the optic nerve to reach them. Below the retina and separated from it by a space is a layer of tissue, the *tapetum lucidum* (*tl*), which serves as a reflector and gives the metallic lustre which is characteristic of the eye of *Pecten*, and below this again comes a pigment-layer (*pg*).

In a small number of forms, e.g. *Arca*, peculiar compound eyes are also found on the edge of the mantle. They form slight rounded elevations and consist of a number of conical retinal cells, each surrounded by a sheath of six cylindrical pigment-cells. Each of these groups of retinal and pigment cells is known as an ommatidium and is separated from the adjoining ones by slender intermediate cells, so that on surface view the composite character of the eye is very distinct.

The nephridia (Fig. 149, *ne*) of the Pelecypoda are always paired, and each consists of a tube bent upon itself lying immediately beneath the pericardial cavity into which one of the limbs opens (np^1), while the other communicates with the suprabranchial chamber (np^2), and so with the exterior. In the simplest forms the entire extent of both limbs is glandular, but in the majority the limb which opens to the exterior loses its glandular character and surrounds to a certain extent the glandular or proximal limb. In addition to these nephridia, frequently known as the organs of Bojanus, pericardial glands are of common occurrence in all but the simplest Pelecypods, and apparently assist the nephridia in their excretory function. They are known also as Keber's organs and consist either of outpouchings of the anterior portion of the pericardial wall into the space between the two walls of the mantle (*Unio, Venus*) or of similar evaginations of the walls of the auricles into the pericardial cavity (*Mytilus*), both methods of formation usually being associated.

The reproductive organs (Fig. 149, *r*) are paired, lying usually in the tissue forming the base of the foot, though extending in some cases into the lacunar spaces between the walls of the mantle (*Mytilus*). They are very richly branched and usually contain in any one individual only ova or spermatozoa, as the case may be, though a number of forms are hermaphrodite—such, for example, as the members of the genus *Cyclas* and some species of the genera *Ostrea* and *Pecten*. The ducts which convey the reproductive elements to the exterior open into the nephridia near their proximal ends in *Nucula* and a few other primitive genera, but more usually open directly into the suprabranchial chamber quite near the openings of the nephridia (Fig. 149, *go*); conditions connecting these two extremes are to be found, as in *Pecten*, where the reproductive ducts communicate with the nephridia near their distal ends, and in *Cyclas* and *Ostrea*, where both nephridial and reproductive openings are contained in a common groove. No complex accessory structures are developed in connection with the reproductive organs, as in some of the Gasteropods, nor is there an intromittent organ in the male, the ova and spermatozoa being usually extruded to the exterior, where fertilization takes place, or else the ova pass from the suprabranchial chamber into the interlamellar spaces of the gill-plates and are fertilized there.

The structure of the gills forms a suitable character for a classification of the Pelecypoda.

1. Order **Protobranchia.**

The gill is a true ctenidium attached by its axis to the roof of the mantle-cavity in its posterior part. In addition to this primitive feature the foot has a creeping surface, the pleural ganglia are not completely united with the cerebral,

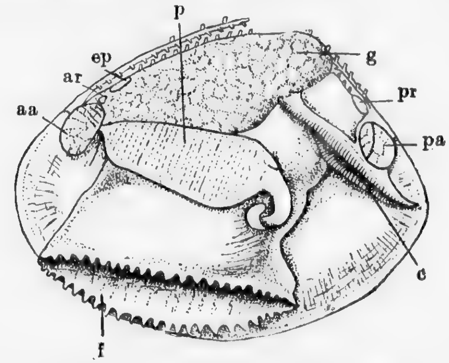


FIG. 151.—*Nucula nucleus* FOR THE LEFT SIDE AFTER THE REMOVAL OF THE LEFT SHELL AND LEFT MANTLE-LOBE (after PELSENEER).

aa = anterior adductor.
ar = anterior retractor pedis.
c = ctenidium.
ep = levator pedis.
f = foot.
g = reproductive organ.
p = labial palp.
pa = posterior adductor.
pr = posterior retractor.

and the reproductive ducts communicate with the proximal portion of the nephridia. To this order, which represents the most primitive Pelecypods, belong the genera *Nucula* (Fig. 151), *Yoldia*, and others.

2. Order **Filibranchia.**

In this group the gill-filaments have elongated considerably and commenced to bend upwards at their ends to form the outer and inner lamellæ (*Anomia; Mytilus, Modiolaria*, the mussels; *Arca*).

3. Order **Pseudolamellibranchia.**

In this the gill-filaments show a tendency to become united together and the inner and outer lamellæ are united (*Pecten*, the Scallop; *Ostrea*, the Oyster).

4. Order **Eulamellibranchia.**

In which the gill-filaments are united to form continuous lamellæ. To this order belong the majority of forms, such as the fresh-water mussels *Unio* and *Anodon*, the small fresh-water *Cyclas*, the hard-shell clam or Quahog *Venus*, the soft-shell clam *Mya*, the razor-shell *Ensatella*, the boring-shell *Pholas*, the ship-worm *Teredo*, and a very large number of other genera.

5. Order **Septibranchia.**

A small group in which the gills are reduced to a muscular perforated septum dividing the suprabranchial chamber from the more ventral mantle-chamber (*Cuspidaria*).

Development and Affinities of the Pelecypoda.—The larva which is characteristic of the Pelecypods resembles a Trochophore very closely indeed and may be described as a Trochophore provided with a bivalved shell. In certain forms the characteristic ciliary bands may, however, be very much reduced, and in the fresh-water mussels (*Unio*, *Anodon*) a remarkable secondary larva known as the *Glochidium* is developed. The ova undergo their development in the interlamellar spaces of the gill plates, and the shell-valves assume a somewhat triangular shape, the apex usually constituting a somewhat curved tooth, while smaller teeth may also be present on the edges. Each mantle-lobe is provided with four tactile papillæ on each side, the slightest stimulation of which causes the shell-valves to close with considerable force and the teeth to adhere to any soft object they come in contact with. By these arrangements the Glochidia are able to fasten themselves to the skin of the fins or to the gills of fishes, where, setting up an inflammation, they become enclosed in a cyst within which the organs assume the adult form, the embryo assuming a truly parasitic habit and drawing nourishment from the tissues of its host. When sufficiently developed the young mussel makes its way out of the cyst and assumes a free mode of life.

As regards the affinities of the Pelecypoda there can be no doubt that between the Protobranchiate forms and the Diotocardiate Gasteropods there are not a few resemblances. They possess a creeping foot, true ctenidia function as gills, the heart is traversed by the rectum, the pleural and cerebral ganglia are distinct, and the nephridia serve to transmit the reproductive elements to the exterior, all of which are also to be found in certain of the Diotocardiates, such as *Haliotis* and *Fissurella*. It may be supposed that the Pelecypods arose from the Gasteropod stem before the asymmetry became developed, and subsequently, by assuming a fixed or limicolous mode of life, a certain amount of degeneration, such as the loss of the radula and of tentacles and cephalic eyes, supervened. The ploughshare-shaped foot is undoubtedly an adaptation to the limicolous habit, and the great development of the gills stands in relation to their mode of obtaining food, the cilia of the gills being responsible for the production of currents sufficiently strong to carry with them diatoms and other small organisms upon which the Pelecypods feed.

V. CLASS **CEPHALOPODA.**

The Cephalopoda are in some respects the most specialized of all the Mollusca, but nevertheless present the primitive bilateral symmetry and arrangement of the structures associated with the mantle-cavity. The visceral hump is enormously developed (Fig. 152), so that the true anterior and posterior surfaces of the body are very long, whereas the ventral surface is comparatively short, the general form of the body being not unlike that of the Scaphopoda. Unlike the members of this latter class the Cephalopods lead, however, a somewhat active existence, some, such as the Squids, swimming actively about in the sea to which they are exclusively confined, while others, such as the Cuttlefishes, have a more creeping habit, though capable of swimming freely. While swimming the animals assume a position in which their longest axis, i.e. the dorso-ventral axis, is more or less horizontal, the true morphological anterior surface thus becoming physiologically the dorsal, and the posterior the ventral surface. In the following description the surfaces will be considered in their morphological relations.

The head is usually somewhat distinctly marked off from the body proper by a neck constriction and bears two usually remarkably-developed and highly-specialized eyes. A peculiar feature of the Cephalopods, and the one which has suggested the name applied to the class, is the fusion with the head of a portion of the foot. The mouth thus becomes situated at the bottom of a funnel-like depression, formed by the foot, whose margins are drawn out into a number of tentacle-bearing lobes or into eight or ten long armlike processes (Fig. 152, *t*) provided with suckers, and serving as powerful

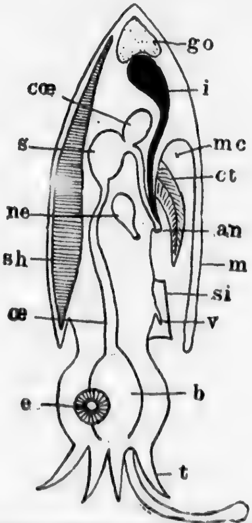


FIG. 152.—DIAGRAM TO SHOW GENERAL PLAN OF STRUCTURE OF A CEPHALOPOD (slightly modified from LANG).

an = anus.
b = buccal mass.
cœ = cæcum of stomach.
ct = ctenidium.
e = eye.
go = reproductive organ.
i = ink-bag.
m = mantle.
mc = mantle-cavity.
ne = nephridium.
œ = œsophagus.
s = stomach.
sh = shell.
si = funnel.
t = tentacle.
v = valve of funnel.

organs of prehension. A second portion of the foot lies in the neck region on the ventral surface and has the form of two folds (*si*), whose edges may be approximated or even fused to form a tube, through which the water contained in the mantle-cavity may be violently expelled, the animal being thereby propelled through the water in a direction of their long dorso-ventral axis. This portion of the foot is termed the funnel and is perhaps equivalent to the epipodium of the Gasteropods. In the majority of forms there projects into the lumen of the funnel a fold (*v*) arising from the body-wall and termed the valve of the funnel. It is probably homologous with the posterior portion of the foot, the metapodium, of the Gasteropoda, so that all portions of the Gasteropod foot are represented in the Cephalopods, the propodium and mesopodium by the arm-bearing portion, the metapodium by the valve just mentioned, and the epipodium by the funnel. In many forms two depressions are to be found on the outer surface of the funnel, which receive two corresponding elevations on the inner surface of the mantle, which thus becomes locked as it were to the funnel during the expulsion of water from the mantle-cavity.

The mantle (*m*) forms a circular fold surrounding the visceral hump, but upon the anterior surface it has usually only a very slight development, while posteriorly there is a wide space, the mantle-cavity (*mc*), between it and the body-wall. Within this space lie the ctenidia (*ct*), and into it the nephridia (*ne*) and the digestive tract open, the excreta being expelled from it during the expulsion of water from the funnel. The mantle-fold is rather thick as a rule, owing to the presence in it of abundant muscle-fibres, by the contraction of which the mantle-cavity may be considerably reduced in size, and frequently there is a special muscular thickening around the edge of the mantle whereby the mouth of the cavity, widely open during the intaking of water, may be firmly appressed upon the funnel during the expulsive act. In the majority of Cephalopods the integument covering the outer surface of the mantle and of the visceral hump is provided with abundant pigment-cells or chromatophores each of which is provided with a muscular arrangement by which its size may be rapidly diminished, remarkable flushes of color passing over the surface of the living animal.

In the *Nautilus* (Fig. 159) a chambered calcareous shell is present having a rather complicated structure which will be described later, and in one or two other living forms, such as *Argonauta* and *Spirula*, an external shell also exists, but in the majority of forms the edges of the mantle close over the shell, which thus becomes internal and takes the form of a plate lying along the anterior surface of the body, being sometimes calcareous as in the common Cuttlefish bone of commerce obtained from the *Sepia* (Fig. 152, *sh*), or else chitinous as in the common Squid, *Loligo*. In connection with the mantle there are also frequently developed finlike expansions with a cartilaginous support and provided with muscles, sometimes running along the sides of the visceral hump or in other cases situated near its dorsal extremity.

The respiratory organs or ctenidia (Fig. 154, *ct*) are present as either one or two (*Nautilus*) pairs of pinnate structures lying in the mantle-cavity. Each consists of a central axis attached throughout its entire length to the body-wall, forming a rather high ridge upon it and containing near its outer edge two blood-vessels running throughout its entire length. The vessel nearer the summit of the ridge is the branchial vein carrying the aërated blood back to the body, and between it and the branchial artery is a cavity or canal which communicates with the mantle-cavity between each pair of branchial pinnæ. These structures arise from near the free edge of the axial ridge, but each is bound to the ridge by a thin triangular membrane so that they possess the form of lamellæ rather than of pinnæ. Near the line of attachment of the axial ridge to the body-wall is a cord of cellular tissue richly supplied with blood coming from the branchial artery, forming what is termed a blood-gland, from which the blood is collected into two longitudinal canals which conduct it back to the heart.

The cœlom of the Cephalopods is characterized by the great development of the pericardial cavity (Fig. 153, *pc*), which recalls the condition found in the Amphineura, and may perhaps be better termed the viscero-pericardial cavity.

In the majority of forms it is a large sac occupying a considerable portion of the apex of the visceral hump and extending ventrally a considerable distance, the more ventral portion being incompletely separated from the more capacious

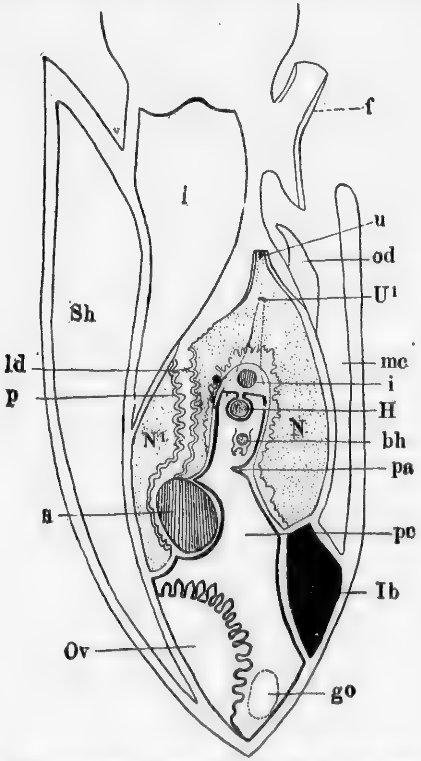


FIG. 153.—DIAGRAM OF BODY CAVITY OF *Sepia* (after GROBBEN).

bh = branchial heart.
f = funnel.
go = reproductive opening into cœlom.
H = heart.
i = intestine.
Ib = ink-bag.
l = liver.
ld = liver-duct.
mc = mantle cavity.
N = nephridium.
od = oviduct.
Ov = ovary.
p = pancreas.
pa = partition partially dividing cœlom.
pc = cœlom.
s = stomach.
Sh = shell.
u = external opening of nephridium.
*U*¹ = opening of nephridium into cœlom.

dorsal portion by a transverse fold or partial partition (*pa*). In *Nautilus* it is placed in direct communication with the mantle-cavity by two minute pores, but in other forms such direct communications do not occur. With a ventral prolongation of the ventral cavity the nephridia (*N*) communicate, and the walls of the cavity fold themselves around the heart (*H*) in the usual manner, and in addition also enclose the branchial hearts (*bh*), becoming thickened and considerably folded in this region so as to form the so-called appendages of the branchial hearts, which are homologous with the pericardial glands of the Lamellibranchs. The wall of the dorsal cavity is in a similar manner folded over the viscera present in that region, and more or less completely encloses the reproductive organs (*ov*) so as to form around them a capsule, sometimes with muscular walls, into the cavity of which the reproductive elements are shed when mature. In one group of Cephalopods, however, the Octopoda, the arrangement departs slightly from this owing to the reduction of the viscero-pericardial cavity to a number of comparatively small canals which constitute the so-called water vascular canals of the older authors. Three of these canals are found on either side of the body, meeting together in a common centre, the nephridia communicating with one, another passing to the branchial heart of its side to form the pericardial gland, while the third extends dorsally to dilate with its fellow of the opposite side into the capsule surrounding the reproductive organs (Fig. 158, *wc*). The general relationships of these canals are evidently comparable with those of the viscero-pericardial cavity of the majority of the Cephalopods, but they differ in one very marked peculiarity, i.e., the heart is not enclosed within their lumen. The tubelike condition of the cavity is evidently a secondary condition, and the exclusion of the heart can be understood as a result of the diminution of the extent of the cavity, when the manner in which it is enclosed, as exemplified by the Solenogastres, is considered.

The schizocœlic portion of the cœlom takes the form partly of lacunar spaces, but partly of blood-vessels with definite walls. To a certain extent the blood system is completely closed, an unusual condition among Mollusca; well-defined veins return the blood carried by the arteries to various portions of the body, definite capillaries connecting the two sets of vessels. A lacunar system also exists, however, so that, while showing a much greater differentiation than the other Mollusca, the Cephalopods yet retain indications of the more primitive arrangement.

The heart consists of a tubular ventricle (Fig. 154, *v*), usually arranged with its long axis directed dorso-ventrally, though in the Octopoda it is transverse, and has opening into it at each side one or two (*Nautilus*) auricles (*au*) which receive the blood from the branchiæ (*ct*). Two principal arteries arise from the ventricle, a larger one running ventrally (*ao*), and a smaller one which runs towards the tip of the visceral hump and supplies the viscera of that region (*ao'*). As already stated, these arteries pass into a fine capillary network from which the veins arise, sinuses, however, intervening in some cases in the course of the latter, and possibly some arterial branches may terminate in such sinuses. The

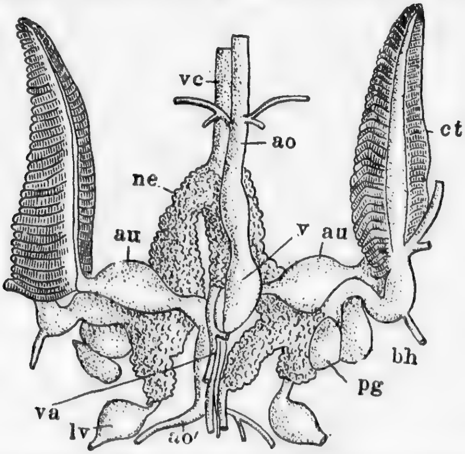


FIG. 154.—CIRCULATORY APPARATUS OF *Sepia* (after HUNTER from OWEN).

ao = anterior aorta.
ao' = abdominal aorta.
au = auricle.
bh = branchial heart.
ct = ctenidium.
lv = lateral vein.
ne = excretory appendage.
pg = pericardial gland.
v = ventricle.
va = abdominal vein.
vc = cephalic vein.

principal venous trunk is the cephalic vein (*vc*), which lies on the posterior side of the œsophagus, and passing dorsally divides into two branches, the venæ cavæ, with each of which an abdominal vein (*va*) unites, the conjoined trunk on each side passing into a contractile dilatation, the branchial heart (*bh*), at the base of the ctenidium of that side. The venæ cavæ and the abdominal veins are covered by a much-folded mass of tissue, the venous appendages (*ne*), which are portions of the nephridia and will be considered in the description of those organs. Mention may also be made here of the pericardial glands (*pg*) attached to the branchial hearts, which have already been described in connection with the visceropericardial cavity.

Slight variations from the arrangement here described may be found in various forms, of which the most important is that found in *Nautilus*, in which, in accordance with the presence of two pairs of ctenidia, each vena cava divides into two branches, one passing to each ctenidium. No branchial hearts occur, and, as has been already mentioned, the ventricle has opening into it two pairs of auricles instead of the single pair usually present.

In the mesodermal tissue of the Cephalopods in various portions of the body there are developed plates and nodules of a consistency resembling cartilage and like it consisting of a hyaline or partly fibrous matrix through which numerous cells with branching processes are scattered. These cartilaginous structures resemble the tissue which is developed in the pharynx of the Gasteropods below the radula, but reach a much more extensive development in the Cephalopods, serving as a protection for some of the more important organs, and also as a *point d'appui* for the various muscles, and therefore constituting a true endoskeleton. In the *Nautilus* there is but a single cartilage which lies on the posterior surface of the œsophagus, being deeply grooved for the reception of the brain and optic ganglia. In other forms, however, the cartilages are more numerous. There is a well-developed cephalic cartilage forming a deeply-concave disk perforated by the œsophagus, and partially enclosing the brain, being also expanded at the sides and hollowed out so as to form a support for the eyes, which are further covered by a pair of plates which project anteriorly and laterally from the anterior margin of the disk. At the base of the arms a brachial cartilage, sometimes united with the cephalic mass, is found which serves for the origin of the brachial musculature, and furthermore a nuchal plate is present lying below the anterior surface of the body just behind the head. In connection with the funnel some plates and nodules are developed, the most important of which is the infundibular cartilage on the posterior (strictly speaking the ventral) surface of the body in the floor of infundibulum, nodules being found below the depressions on the side of the infundibulum and the corresponding elevations of the mantle which have already been described as interlocking during the expulsion of water through the funnel. Finally, it may be mentioned that the centre of each fin is occupied by a cartilaginous plate which serves for the origin of the muscles which move the fin.

In harmony with the peculiar modification of the foot there is a considerable amount of differentiation of special muscles in the Cephalopods, which pass from cartilage to cartilage or from the shell to the various cartilages. Leaving aside the general musculature of the mantle and of the arms, mention may be made of the three or four strong retractor muscles, which pass from the shell to the cephalic cartilage and are sometimes fused together to form a single strong muscle which serves to retract the head; the collaris, which runs on either side of the neck from the infundibular cartilage to be inserted into the sides of the nuchal cartilage; and finally the adductors and depressor of the funnel, which pass respectively from the cephalic cartilage and the shell to be inserted into the infundibular cartilage. Considerable variation is to be found in the arrangement of muscles in various forms, but the typical arrangement may be regarded as being somewhat as described.

Like the other organs the digestive system presents a considerable amount of differentiation. The mouth opens in the centre of the disk which bears the arms or tentaculiferous lobes, and is guarded by two strong chitinous or partly calcareous (*Nautilus*) jaws resembling in form the beak of a parrot.

It leads into a muscular pharynx (Fig. 152, *b*), upon the floor of which lies the characteristic molluscan radula, while into its cavity the ducts of one or two pairs of salivary glands open. Succeeding the pharynx is a tubular œsophagus (*œ*) which in some forms is provided with a lateral diverticulum, the crop, and which terminates below in the large pyriform stomach (*s*). The intestine leaves the stomach close to the entrance of the œsophagus, and a pouchlike structure, in some forms prolonged into a spiral cæcum (*cœ*), is to be found either communicating with the stomach close to this point or else opening into the proximal portion of the intestine (*Nautilus*). Into this cæcum the two ducts from the large digestive glands, or so-called liver, open, their walls being in the majority of cases provided with sacculations arranged in bunches and constituting the pancreas, a structure which in *Loligo* (Fig. 153, *p*) is imbedded in the thickened walls of the ducts or else, as in *Octopus*, attached to the digestive gland in the region where its ducts arise. From its origin in the stomach the intestine passes ventrally, the entire tract having thus a V-shaped arrangement, and opens into the mantle-cavity on the summit of a papilla situated a short distance from the dorsal end of the infundibulum. From each side of the anal papilla a fleshy appendage arises, the anal valve, which in some forms may be drawn down so as to completely close the anal opening.

In connection with the posterior portion of the digestive tract there is found in all Cephalopods except *Nautilus* a saclike gland (Fig. 152, *i*) which secretes a dark pigment and is known as the ink-bag, the animal discharging the ink into the surrounding water to conceal its retreat when alarmed. It arises as a saclike diverticulum of the rectum close to its termination and, elongating, becomes differentiated into a duct of considerable length opening into the terminal portion of the rectum and closed by a circular band of muscle-fibres which surround it near its opening. The more or less globular extremity of the diverticulum becomes differentiated into (1) a cavity which serves as a reservoir for the inky secretion manufactured in (2) a special glandular region, traversed by a series of trabeculæ lined by the secreting cells.

The nervous system of the Cephalopods shows a high degree of concentration, the various ganglia being more or less fused with one another to form a mass surrounding the œsophagus just behind the pharyngeal mass. In *Nautilus* this mass takes the form of two rings surrounding the œsophagus, united in front but widely divergent behind, and in which the various ganglia are but indistinctly indicated, the condition which occurs in *Chiton* in this respect being recalled. That portion of the ring which lies in front of the œsophagus represents the cerebral ganglia; the lateral portions of the more ventral of the two rings found on the posterior surface are the pedal ganglia, giving rise to the nerves to the pedal lobes and the infundibulum; while the more dorsal posterior ring represents the combined visceral, parietal, and pleural ganglia. In other forms the ganglia become more perfectly marked off and at the same time more concentrated. A cerebral ganglion (Fig. 155, *c*) is always distinguishable, and with it are connected pleuro-parieto-visceral (*pl* and *v*) and pedal (*p* and *p′*) ganglia; the latter, however, are usually divided into two portions—a more ventral mass (*p′*) which sends branches to the armlike prolongations of the pro- and mesopodium and which is hence termed the brachial ganglion, and a more dorsal one (*p*) which supplies the infundibulum and is known as the pedal ganglion proper. A study of a number of different forms shows clearly that the brachial ganglion is merely a separated portion of the pedal, and that the arms are to be considered portions of the foot and are not cephalic appendages. At the sides of the cerebral ganglia there are to be found a pair of large ganglia (*op*) which stand in relation to the eye and are termed the optic ganglia; they are undoubtedly specializations of the cerebral ganglia, owing their separate exist-

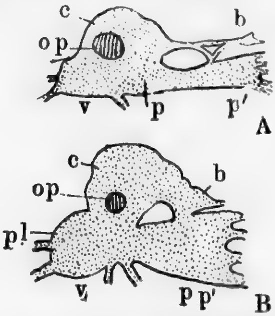


FIG 155.—NERVOUS GANGLIA OF (*A*) *Loligo* AND (*B*) *Octopus* (after PELSENEER).

b = buccal ganglion.
c = cerebral ganglion.
p = pedal ganglion.
p′ = brachial ganglion.
op = optic ganglion.
v = pleuro - parieto - visceral ganglion.

ence to the remarkable development and differentiation of the eye which is found in the majority of the Cephalopods.

A sympathetic system of nerves is well developed and consists of one or two pairs of buccal ganglia (*b*) innervating the large pharyngeal mass and united to the cerebral ganglia by connectives and giving rise to a strong nerve which runs dorsally along the œsophagus to end in a large gastric ganglion from which nerves pass to the viscera. Mention should also be made of two other ganglia, the ganglia stellata, which belong to the central system and are situated in the lateral portions of the mantle, being united with the pleurovisceral ganglia by strong nerves; they correspond probably with the parietal ganglia of the Gasteropods, sending branches to the tissues of the mantle.

The special sense-organs are exceedingly well developed, and especially is this the case with the eyes. In *Nautilus*, however, the eye (Fig. 156, *A*) stands on a much lower grade of organization than that of the other Cephalopods, consisting of a cup lined by a retina composed of several layers and richly supplied with nerves. The outermost layer consists of rodlike bodies (*r*) below which is a layer of pigment (*pg*), below which again lies a layer of ganglion-cells (*g*). No refractive structures are, however, present, the cavity of the cup communicating freely with the

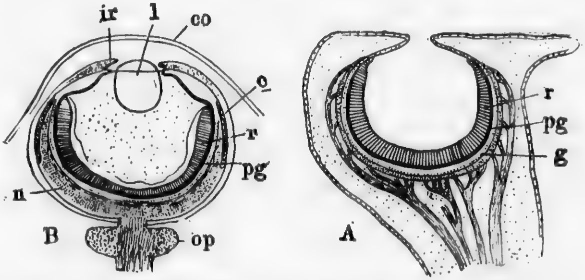


FIG. 156.—*A*, Eye of *Nautilus* (modified from HENSEN); and *B*, of *Loligo*.
c = cartilage.
co = cornea.
g = layer of ganglion-cells.
ir = iris.
l = lens.
n = nerve-layer.
op = optic nerve and retinal ganglion.
pg = pigment-layer.
r = layer of rods.

external water through a small circular opening in the front flattened wall of the cup. The eye is a camera constructed on the "pin-hole" type, the image being defined by the exclusion of all the more divergent rays of light which pass in from the object towards the eye.

In the remaining forms the eyes (Fig. 156, *B*) are large globes imbedded in an orbit formed by the lateral portions of the cephalic cartilage and its processes. The retinal portion of the eye closely resembles that of *Nautilus*, consisting of an external layer of rods (*r*) bounded beneath by a pigment-layer (*pg*) beneath which is a nerve-layer (*n*) enclosed within a connective tissue-sheath in which cartilage (*c*) is developed. The optic nerve dilates into a retinal ganglion before being distributed to the retina, the rods of which, it will be noted, are turned towards the source of light. The eye-cup differs, however, from that of *Nautilus* in being completely closed, and the cells which form the outer and inner layers of the outer wall of the cup secrete chitinous material which acts as a lens (*l*), forming a powerful biconvex condenser. In addition to this the eye is further complicated by the development of a series of folds from the skin in its neighborhood. One such fold is developed from the front wall of the optic sac, surrounding the region occupied by the lens and forming an iris (*ir*), the circular opening in its centre corresponding to the pupil of the Vertebrate eye. A second likewise forms nearer the base of the optic sac and, growing forward, may enclose a space bounded behind by the iris and lens, resembling the anterior chamber of the Vertebrate eye, the portion of the fold immediately in front of the lens becoming transparent and forming a cornea (*co*). The anterior chamber is not, however, closed in all forms, but remains in communication with the exterior by an aperture produced by a failure of the edges of the fold to unite completely. Finally, in some forms other folds, which from analogy have been termed eyelids, develop.

The resemblance of such an eye to that found in the Vertebrates is exceedingly striking, but a detailed study of the structure and mode of origin of the various parts demonstrates conclusively that the similarities are analogical only and not homological. One of the most important of the differences is found in the arrangement of the layers of the retina, the rods being turned towards the light as is usual in Invertebrate eyes, while in the Vertebrates they are reversed, the nerve-fibre layer lying above them, the light of necessity penetrating it before reaching the rods. The structure of the lens is again very different, being cellular and formed as an invagination of the ectoderm in the Vertebrates, while in the Cephalopods it is a cuticular structure. These are fundamental differences and may suffice to show what is meant, but many other dissimilarities may readily be found.

Otocysts also occur imbedded in a capsule forming part of the cephalic cartilage. They have the characteristic Molluscan form and receive a large nerve arising from the cerebral ganglion. Osphradia occur only in *Nautilus*, where they form a pair of sensory papillæ one of which lies at the base of each of the more ventral ctenidia. Other Cephalopods, though lacking these structures, are yet provided with special olfactory organs in the form of a pair of fossæ or grooves lined by ciliated and sensory cells and situated above the eye in the position occupied by the eye-tentacles of *Nautilus* (see p. 358), from which they may possibly have been derived.

The excretory organs consist of two comparatively large sac-like nephridia except in *Nautilus*, in which, in harmony with the number of ctenidia and auricles, there are four. In *Octopus* and the other members of the group Octopoda the two nephridia are quite separate from one another, but in the group Decapoda, to which *Loligo* and *Sepia* belong, they are placed in communication with one another by transverse canals one of which may be produced dorsally into a large sac occupying a great portion of the anterior region of the body. The venæ cavæ and branchial veins lie between the walls of this anterior sac and the paired posterior nephridia, and along the course of the veins the walls of the excretory sacs are richly folded (Fig. 154, *ne*), constituting the venous appendages, for a long time considered to be the excretory organs in their entirety. The posterior paired nephridia present the same relations to the exterior and to the enterocœl which exist in other Mollusca, opening by two distinct apertures into the mantle-cavity on the one hand, and on the other communicating with the large enterocœl which has been shown to be the equivalent of the pericardial cavity of the Gasteropods and Pelecypods.

The reproductive organs are situated near the dorsal extremity of the visceral hump. The sexes are always separated in different individuals, there being occasionally well-marked differences between the two sexes of the same species, as in *Argonauta*, the female of which possesses a well-developed shell which the male lacks. The ovary (Fig. 157, *ov*) is single and is enclosed in a capsule (*c*) formed by the walls of the enterocœl or viscero-pericardial cavity, into which the organ seems to project, though morphologically it is entirely outside it.

The germ-producing region is nearly always the anterior surface of the organ, the stalked ova surrounded by their follicle-cells projecting forward into the capsule, into the cavity of which, i.e. into the viscero-pericardial cavity, they burst when mature. In some forms the germ-producing surface becomes more highly folded and more or less dendritic in form, the area over which the ova are formed becoming thus much greater. The ova reach the exterior after they have passed into the cavity of the capsule by means of one or two complicated ducts (*od*) opening into the mantle-cavity. In *Nautilus* two ducts are present, that of the left side, however, being non-functional, and in the Octopoda and some Decapods, such as *Ommastrephes*, both ducts are present. In other forms but a single duct persists, which, contrary to what occurs in

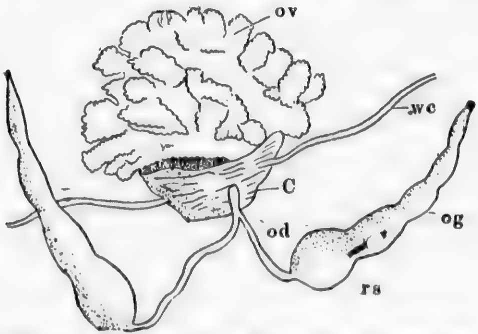


FIG. 157.—FEMALE REPRODUCTIVE ORGANS OF *Tremoctopus violaceus* (after BROCK).

c = capsule.
od = oviduct.
og = oviducal gland.
ov = ovary.
rs = seminal receptacle.
wc = cœlomic canal.

Nautilus, is that of the left side. The oviduct opens into the mantle-cavity at the extremity of a well-marked papilla, its terminal portion being richly supplied with glands, and in addition in some forms two small pear-shaped glands are attached to it in this region. In connection with the female ducts there should be mentioned a pair of glands which take part in the formation of the investments of the ova, but which open quite separate from the oviduct into the mantle-cavity. These are the nidamental glands which are present in the majority of forms, excluding the Octopoda, and consist of a pair of large pyriform structures lying on the posterior surface of the visceral mass; in connection with them in some forms are developed accessory nidamental glands consisting of a central and two lateral portions whose ducts open into the mantle-cavity in close proximity to those of the nidamental glands proper. As stated, the gelatinous mass within which the ova are imbedded is probably manufactured by these glands.

The testis in its general relations resembles the ovary, being single and enclosed in a capsule which is a portion of the viscero-pericardial cavity. The organ is attached to the wall of the capsule by a thin band of tissue and is in most cases almost completely surrounded by the capsule, into the cavity of which the spermatozoa are shed when mature. From the wall of the capsule the vas deferens arises and is usually a single tube opening upon the left side of the body into the mantle-cavity. In *Nautilus* there are, as in the female, two ducts, the right, however, being functionless, but in other forms a paired arrangement is very rare. The proximal portion of the duct is a coiled vas deferens, which opens into a thick-walled glandular seminal vesicle which on its part by means of a narrow duct passes into a saclike structure known as Needham's pouch which finally passes into the muscular penis. In most forms the duct connecting the seminal vesicle with Needham's pouch receives the secretion of a special gland known as the prostate.

The majority of the accessory structures connected with the male ducts are concerned in the formation of cases or spermatophores in which a number of spermatozoa are enclosed. Such cases are cylindrical structures with a double wall, and are provided at one extremity with a somewhat complicated apparatus for the ejection of the spermatozoa. The exact method of their formation is not understood, but apparently the seminal vesicles and the prostate play an important part in the process, the Needham's pouches being a reservoir in which they may be stored up until required for fertilization.

Since the genital capsule is a portion of the viscero-pericardial cavity, and the reproductive ducts are continuations of its walls, these structures must also be regarded as prolongations of the enterocœl; and indeed secondary communications may exist between them and the viscero-pericardial cavity proper. The genital capsule is not completely separated off from the rest of the enterocœl, so that it might be possible for the reproductive elements to pass from its cavity into the viscero-pericardial cavity proper, and so to the exterior through the nephridia, though this method of exit does not seem to be made use of.

A remarkable modification of one of the armlike processes of the foot occurs in the males of certain species in connection with reproduction. The arm—in *Tremoctopus* and *Philonexis* the third arm of the right side of the body counting from the anterior mid line, in *Argonauta* (Fig. 158) the third of the left side—is at first enclosed within a sac, by the bursting of which it becomes free, the walls of the sac being reflected back so as to form a pouch which in some unexplained manner receives a

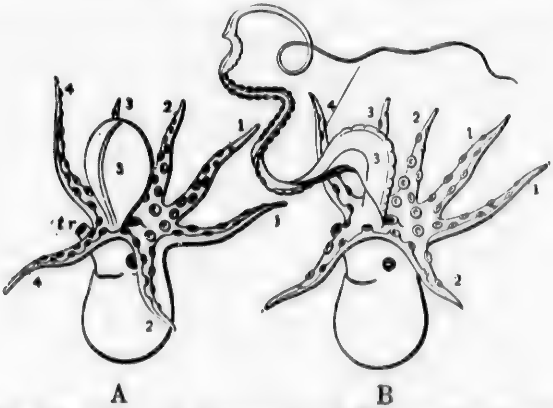


Fig. 158.—Male of *Argonauta* with Hectocotylized Arm (after H. Muller from Hatschek).

A = arm still enclosed within a membranous sac.
B = arm freed from the sac.

spermatophore. The terminal portion of the arm, which is traversed throughout its entire length by a canal, is developed into a long terminal filament through which the spermatozoa may pass. During copulation the arm is probably thrown off and passes into the mantle-cavity of the female, the manner in which the spermatozoa reach the ova being, however, not yet understood. When first discovered in the mantle-cavity of a female the arm was regarded as a parasitic worm, and the name *Hectocotylus* was applied to it—a term which is still retained on account of its convenience. In other genera of Cephalopods one arm is generally peculiarly modified in the male—in the Decapoda usually the fourth of the left side and in the Octopoda usually the third of the right side, though frequent exceptions are found. This arm is termed the hectocotylized arm, though it is doubtful whether it takes any part in copulation.

As will be seen from the above description the genus *Nautilus* differs in many important particulars from the remaining genera of Cephalopods, and the class is therefore divided into two orders.

1. Order **Tetrabranchia.**

This order, of which the genus *Nautilus* (Fig. 159) is the sole living representative, was in former periods of the earth's history the dominant group of the Cephalopods—the Orthocerites of the Palæozoic and the Ammonites of the Mesozoic being extinct members of it. It is characterized by its members possessing four ctenidia, four auricles to the heart, and four nephridia; and in addition there may be mentioned, as further peculiarities, the presence of paired reproductive ducts, of which the right one alone is functional, and also of direct communication of the viscero-pericardial cavity with the exterior by two pores, and by the occurrence of a single pair of osphradia. For a more detailed account of the peculiarities of *Nautilus* the preceding general description may be consulted. It remains to discuss here the shell and the structure of the foot-lobes—structures which, with the other characters mentioned, serve to distinguish *Nautilus* from all its living congeners.

The shell is voluminous, coiled, and calcareous, its cavity being divided by a series of transverse partitions into a number of chambers, in the last—that is to say, the youngest—of which the animal lives, while the remaining ones are filled with gas. The centre of each partition is perforated, and through the opening there extends to the tip of the shell a prolongation of the body of the animal, termed the sipuncle.

The foot of *Nautilus*, or at least that portion of it which fuses with the head, has already been described as forming a number of tentaculiferous lobes. These lobes are arranged in the female in two series—one ventral, consisting of three lobes which immediately abut upon the mouth, and a more dorsal ringlike lobe the anterior portion of which is developed into a hood (4) which arches over and protects the retracted tentacles. Around the margins of both the ventral and dorsal lobes are arranged the tentacles, each of which is filiform and capable of being withdrawn into the basal portion, which thus serves as a sheath. In addition to these tentacles two other tentacles are found in close proximity to the eye, one being on its ventral side and the other on its dorsal. In the male the arrangement is very similar, except that the median lobe of the ventral series is transformed into a lamellated structure and does not bear tentacles, while a portion of each of the lateral lobes of the inner series is sepa-

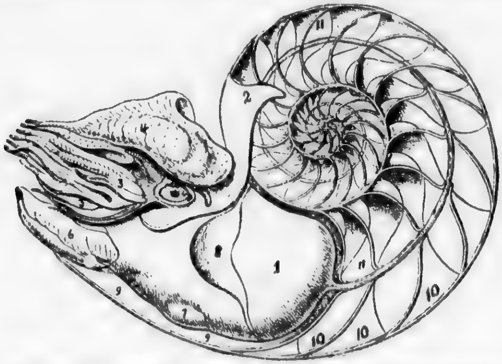


Fig. 159.—*Nautilus pompilius*,—Female, with the Shell sectioned Longitudinally to show its Internal Structure (after Leunis from Hertwig).

1 = mantle.
2 = dorsal lobe of mantle.
3 = tentacles.
4 = head-cap.
5 = eye.
6 = funnel.
7 = nidamental gland.
8 = shell-muscle.
9 = terminal chamber of shell.
10 = partitions between the various chambers.
11 = sipuncle.

rated from the rest of the lobe—that of the left side becoming modified into a conical structure, lamellated at the extremity and destitute of tentacles, forming what is termed the spadix, probably homologous with the hectocotylized arm of the male Octopods and Decapods.

2. Order **Dibranchia.**

The members of this order, which includes the majority of living Cephalopods, possess but a single pair of ctenidia, nephridia, and auricles, and lack the direct communication of the viscero-pericardial cavity with the exterior as well as the osphradia which occur in *Nautilus*. The portion of the foot which is fused with the head is drawn out into a number of arms provided with suckers, which seem to represent the tentacles and their sheaths found in *Nautilus*. The suckers are very numerous and may be arranged in from one to four rows on the ventral surface of the arms, the margin of each sucker being in some forms strengthened by a horny ring, which may be toothed. The number of the arms varies, being either eight or ten; and, since, other structural differences are associated with this difference, the order may be divided into two suborders—the Octopoda with eight arms, including the genera *Octopus*, *Tremoctopus*, and *Argonauta* (Fig. 153), and the Decapoda with ten arms, the genera *Spirula*, *Ommastrephes*, *Sepia*, and *Loligo* (Fig. 160) belonging to this group.

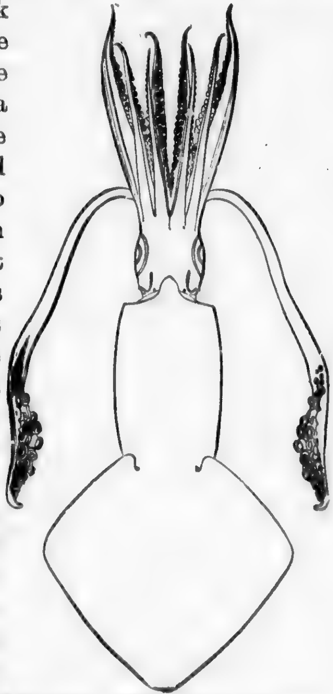


FIG. 160.—*Loligo pallida*, DORSAL VIEW (after EMERTON from VERRILL).

In the Decapoda the ten arms are not of equal size, one on each side of the head, the fourth, counting from the anterior mid-line, being longer than the rest, usually destitute of suckers except towards the tip, and in most species kept retracted within a groove on each side of the head except when required for prehension. They are all good swimmers, and the body is elongated and provided with lateral fins of greater or less extent.

A shell is present in the Decapoda, but shows a great reduction in size and complexity from that of the Tetrabranchiates; and in order to understand its homologies in the different genera it will be necessary to obtain an idea of its form in the fossil members of the group which occur in the Mesozoic rocks forming the family Belemnitidæ. In the genus *Belemnites* (Fig. 161, *B*), for instance, the shell consisted of a terminal conical solid portion, termed the rostrum (*r*), the base of which was hollow and contained a chambered shell, the phragmacone (*ph*), corresponding to the *Nautilus* shell, the anterior portion of the last chamber of this being elongated into a broad flat process termed the proöstracon (*pr*). By various modifications of this structure the shells of the different living Decapods have been developed. In *Spirula* the shell is coiled into a spiral and is partly enclosed by the mantle, the rostral and proöstracal portions having disappeared. In all other forms the shell has a more or less flattened form and becomes completely enclosed within the mantle, folds of which grow up around it. In *Sepia* (Fig. 161, *A*) the proöstracon becomes almost obliterated and the rostrum (*r*) is exceedingly small, the phragmacone (*ph*) forming the principal bulk of the shell. This, however, has become very much modified—that portion of it which lies posterior to the sipuncle (*s*) ceasing to develop, or rather becoming exceedingly compact by the various partitions lying in close contact with one another without any intervening air-chambers. These chambers are, however, developed in the portion anterior to the sipuncle, but are comparatively flat and traversed by calcareous spicules, so that the shell has a somewhat spongy appearance and is exceedingly light. In other forms, however, the proöstracon is the portion that persists, the rostrum and phragmacone both disappearing (Fig. 161, *C*). —

that finally nothing is left but a plate imbedded in the mantle, formed entirely of chitinous material and destitute of any calcareous substance. This forms the so-called "pen" of such forms as *Loligo* and *Ommastrephes* (Fig. 161, *D*), a slight thickening of the dorsal end of it in some forms representing the remains of the phragmacone.

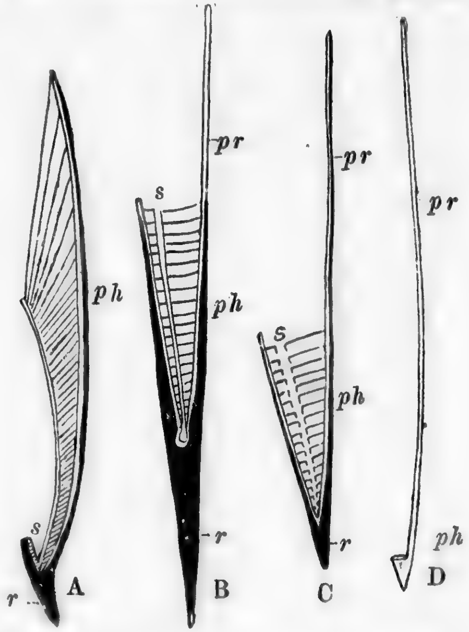


Fig. 161.—Diagrams of Shell of *A*, *Sepia*; *B*, *Belemnites* (fossil); *C*, *Ostracoteuthis* (fossil); and *D*, *Ommastrephes* (after Lang).

ph = phragmocone.
pr = proöstracon.
r = rostrum.
s = sipuncle.

In the Octopoda the eight arms are practically equal in length, and the body is more massive than in the Decapods and less suited for active swimming. The visceral hump is a more or less globular mass, destitute as a rule of lateral fins, and in all forms a shell comparable to that of the Decapods is wanting. In the females of *Argonauta*, however, a nonchambered calcareous shell is present, to which the body of the animal does not closely adhere, but which is held in position by the broad plate-like anterior arms which embrace it.

It seems to be a secretion of the ectoderm of the mantle and visceral hump, the anterior arms contributing only a thin external layer.

Development and Affinities of the Cephalopods. — The ova of those Cephalopods which have been studied are richly provided with yolk, in consequence of which the development becomes considerably modified, definite traces of the Veliger condition being entirely lost. It seems clear, however, from the marked development of the head, the presence of a radula, and the general arrangement of the viscera, that the ancestry of the group is to be sought for among the primitive Gasteropods, but in forms more primitive than any existing forms. The symmetrical shape of the body and the character of the viscero-pericardial cavity suggests forms intermediate in development between the Amphineura and the Diotocardiate Prosobranchs.

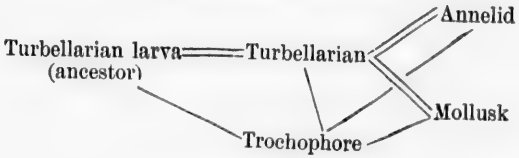
So far as the various groups are concerned there can be little doubt but that the Tetrabranchs are the more primitive forms, showing as they do less specialization of the foot, what must be considered a more primitive shell, and a more general tendency towards a paired arrangement of the organs than is found in the Dibranchs. The duplication of the ctenidia and nephridia must, however, be considered a secondary acquisition. The Decapods, again, seem to be on the whole more primitive than the Octopods, the character of the cœlom and the presence of a shell in the former being points to which attention may be called in this connection.

The Affinities of the Mollusca.—Attention has already been called to the similarity of the typical Gasteropod and Pelecypod larvæ to the Annelid Trochophore, and the evident conclusion has been pointed out that the Annelids and Mollusca are to be traced back to a common ancestor represented by the Trochophore. It is difficult otherwise to understand the remarkable similarity which exists between the two larvæ—similarities, including not only the general arrangement of the locomotor cilia, but extending as well to internal organs, such as the nephridia. In two respects, however, the Molluscan Veliger differs from the Annelid Trochophore; it possesses a shell and a foot. These features are, however, readily explicable as a throwing back in the ontogeny of important structures originally developing at a much later period in the life of the animal—a phenomenon of by no means unfrequent occurrence. It must be admitted, however, that frequent modifications of the Trochophore arrangement are to be found, as has been indicated in the descriptions of the Amphineura, and these become especially interesting from the fact that in the former a primitive arrangement of the parts of the body must be recognized. If the Trochophore represents an ancestor, then it might be expected that it would be found more perfectly represented in the Amphineura than in the highly specialized Gasteropods, or even than in the Pelecypods.

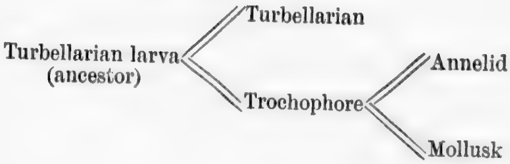
It is important, then, that the possibility of some of the similar structures of the Trochophore and Veliger having been independently acquired should be kept in mind, especially in view of another idea as to the genealogy of the Mollusca which has been advocated by certain authors. According to this theory they have sprung from Turbellarian-like ancestors, the creeping surface of the worm having become more muscular, and so having given rise to the foot of the Mollusk, the dorsal region of the body elevating into the visceral hump. The nervous system of the Amphineura, with its ladder-like arrangement, might readily be deduced from the arrangement found in the Platyhelminths, and thus many points on which the Trochophore theory throws no light become intelligible.

This theory concerns itself mainly with the adult forms, yet it is not impossible that a reconciliation between it and the Trochophore theory may be possible. It has already been pointed out that the Trochophore may possibly be the representative of a Turbellarian larva, and the same idea may be applied to the Veliger. In other words, it is possible that the Mollusca may have been derived from the Turbellaria, and that the ancestral worms possessed in their life-history a larva which, independently of the adults, underwent a series of modifications leading to the Veliger. The Veliger would then be the descendant of a Turbellarian larva, while the adult Mollusk would be directly descended from the Turbellarian. This view may be contrasted with that which regards the Trochophore (including the Veliger under this term for convenience) as the ancestor by means of the following scheme:

TURBELLARIAN THEORY.



TROCHOPHORE THEORY.



SUBKINGDOM METAZOA.

TYPE MOLLUSCA.

I. Class **Amphineura.**—Visceral hump not developed; bilaterally symmetrical; shell represented by scattered spicules or by a series of calcareous plates; anus terminal.

1. Order *Solenogastres.*—Shell represented by scattered calcareous spicules. *Neomenia*, *Proneomenia*, *Chætoderma*, *Dondersia.*

2. Order *Polyplacophora.*—Shell formed by eight plates on dorsal surface of body. *Chiton*, *Trachydermon*, *Chitonellus.*

II. Class Gasteropoda.—Visceral hump usually well developed; body asymmetrical; shell univalved and usually spirally coiled, sometimes absent; anus not terminal.

1. Order *Prosobranchia.*—Ctenidia present, situated in front of the heart; auricle in front of ventricle; mantle edge not fused with body.

Heart with two auricles; two nephridia (*Diotocardia*). *Haliotis*, *Turbo*, *Trochus*, *Neritina*, *Pleurotomaria*, *Fissurella*, *Patella*, *Acmæa.*

Heart with a single auricle and a single nephridium (*Monotocardia*).

Dentition tænioglossate.

With creeping habit. *Cypræa*, *Paludina*, *Natica*, *Ampullaria*, *Littorina*, *Cyclostoma*, *Calyptræa*, *Strombus.*

With pelagic habit (*Heteropoda*). *Atalanta*, *Carinaria*, *Pterotrachea.*

Dentition ptenoglossate. *Ianthina*, *Scalaria*, *Solarium.*

Dentition rachiglossate. *Fusus*, *Buccinum*, *Nassa*, *Murex*, *Purpura*, *Oliva*, *Marginella.*

Dentition toxiglossate. *Terebra*, *Conus*, *Pleurotoma.*

2. Order *Opisthobranchia.*—Ctenidia frequently absent, when present behind the heart; auricle behind ventricle; mantle when present not fused by its edges to body-wall; shell frequently absent.

Mantle present (*Tectibranchia*).

Foot with broad flat sole; with creeping habit. *Bulla*, *Janus*, *Aplysia*, *Pleurobranchus.*

Foot with winglike parapodia, pelagic (*Pteropoda*).

With shell (*Thecosomata*). *Limacina*, *Styliola*, *Cymbuliopsis.*

Without shell (*Gymnosomata*). *Pneumoderma*, *Clione.*

Mantle not developed (*Nudibranchia*). *Pleurophyllidia*, *Phyllirhoë*, *Limapontia*, *Doris*, *Æolis*, *Facellina.*

3. Order *Pulmonata.*—Ctenidia wanting; mantle fused by its edges to body-wall; terrestrial or aquatic.

Eyes at base of tentacles (*Basommatophora*). *Limnæa*, *Physa*, *Planorbis.*

Eyes at tip of tentacles (*Stylommatophora*). *Helix*, *Limax*, *Arion*, *Vaginula*, *Daudebardia*, *Onchidium.*

III. Class Scaphopoda.—Visceral hump developed; bilaterally symmetrical; shell cylindrical, open at both ends. *Dentalium*, *Siphodentalium*, *Cadulus.*

IV. Class PELECYPODA.—Visceral hump not developed; bilaterally symmetrical; mantle forms two lateral folds; shell bivalved; anus terminal.

1. Order *Protobranchia.*—Gill a true ctenidium; pleural ganglia not united to cerebral. *Nucula*, *Yoldia*.
2. Order *Filibranchia.*—Gill-filaments elongated and bent upwards at ends; cerebral and pleural ganglia fused. *Anomia*, *Mytilus*, *Modiolaria*, *Arca*.
3. Order *Pseudolamellibranchia.*—Gill-filaments turned up at ends and with interlamellar junctions; cerebral and pleural ganglia united. *Pecten*, *Ostrea*.
4. Order *Eulamellibranchia.*—Gill filaments united to form a plate-like gill; cerebral and pleural ganglia united. *Venus*, *Mya*, *Ensatella*, *Pholas*, *Teredo*, *Unio*, *Anodon*, *Cyclas*.
5. Order *Septibranchia.*—Gill reduced to a muscular perforated septum between the mantle and suprabranchial chambers. *Cuspidaria*.

V. Class CEPHALOPODA.—Visceral hump developed; bilaterally symmetrical; mantle a circular fold; foot (*propodium* and *mesopodium*) forming arm-like structures provided with suckers and surrounding the mouth.

1. Order *Tetrabranchia.*—With four ctenidia and with external chambered shell. *Nautilus*.
2. Order *Dibranchia.*—With two ctenidia; shell if external not chambered, usually internal.
   With eight arms to foot (*Octopoda*). *Argonauta*, *Octopus*, *Tremoctopus*, *Philonexis*.
   With ten arms to foot (*Decapoda*). *Spirula*, *Sepia*, *Loligo*, *Ommastrephes*.

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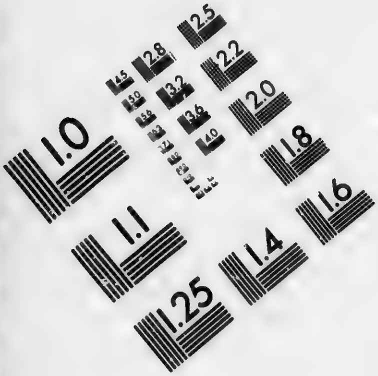
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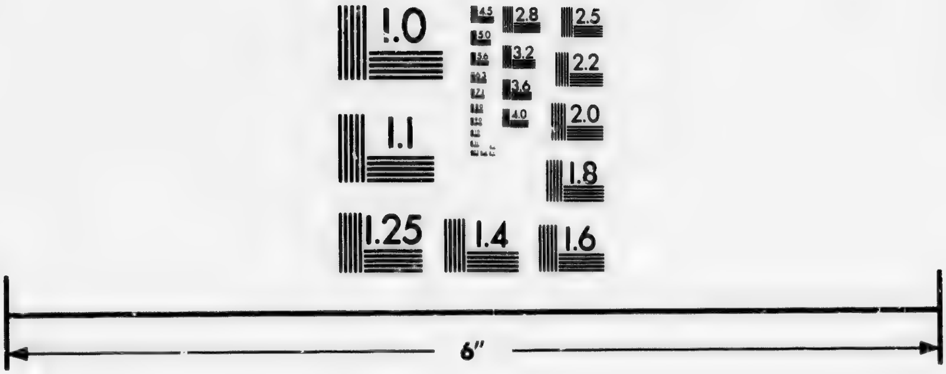
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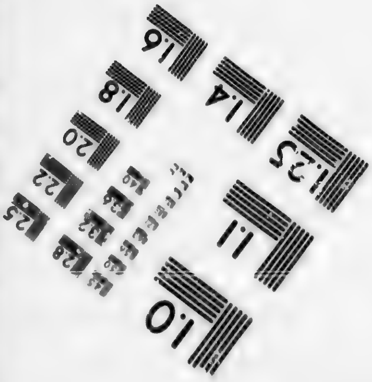
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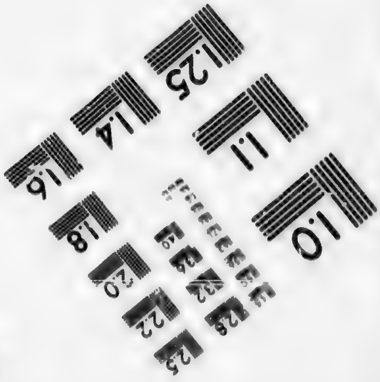
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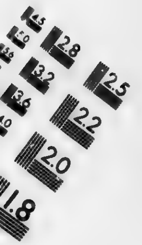
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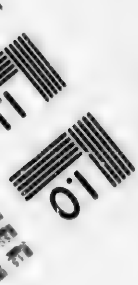
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CHAPTER XIII.

TYPE CRUSTACEA.

THE group Crustacea includes a very large number of forms, most of which are marine, though many are found in fresh water and a few are even terrestrial. A great diversity of form is found in the various members of the group, but at the same time the general structure, except in forms degenerated by parasitism, shows comparatively close similarity throughout.

The body is enclosed in a thick chitinous cuticle which not infrequently becomes hardened by the deposition of calcareous matter in it, producing what may almost be considered a shell and giving origin to the name applied to the group. This covering serves not only for protection, but also as a *point d'appui* for the insertion and origin of muscles. Where it reaches a considerable thickness it becomes more or less regularly divided into segments, separated by intervals in which the cuticle remains thin, so that movement of the various segments upon each other are possible.

As a rule there is attached to the sides of each of these segments an appendage, also inclosed in a more or less thick cuticle and jointed, this jointed character having suggested the reference of the Crustacea together with the Arachnida and Tracheata to a single group termed the Arthropoda. An examination of the internal parts, especially of the nervous system, shows that these various body-segments are in reality metameres, and that the Crustacean is, like the Annelid, a metameric organism. A characteristic of the Crustacea, however, is a tendency towards a greater differentiation and consolidation of the metameres than is found in the Annelida, a tendency especially well marked in the anterior region of the body, where a varying number of the metameres fuse more or less perfectly together to form a distinct head, bearing the principal sense-organs and the organs of mastication (Fig. 162), there being behind this head, more or less perfectly distinguishable, a thorax and an abdomen. Judging from the number of pairs of appendages arising from this head region it seems that the typical number of metameres consolidated to form it is five, but to these there must be added an anterior segment which does not bear appendages but upon which the eyes are developed. To these six somites there are added, especially in the more highly-differentiated forms, a number of additional metameres which properly belong to the thorax, the apparent extent of the head region being thus increased.

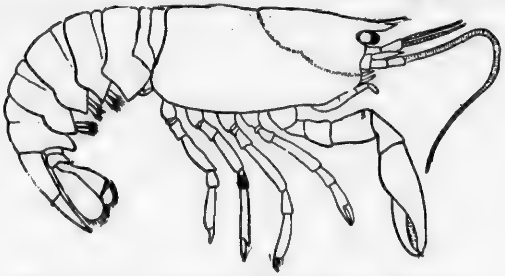

FIG. 162.—A DECAPOD CRUSTACEAN, *Cambarus*.

There is indeed throughout the Crustacea a tendency towards what has been called "cephalization," i.e., a condensation of the anterior metameres, and as a rule the higher the form the greater is this condensation and the greater the apparent extent of the head region. The number of segments composing the thorax and abdomen is exceedingly variable in the lower forms, but in the higher there are constantly eight thoracic and seven abdominal segments, the posterior one, termed the telson, being alone destitute of appendages. Frequently, especially in the higher forms (Fig. 162), the thoracic segments consolidate to a greater or less extent, the segmentation of this region of the body being indicated in some forms only by the appendages and the nerve-ganglia, and furthermore lateral folds of the body-wall may project backwards from the sides and dorsum of the head or anterior thoracic regions, enclosing the thorax or even the entire body in a firm carapace or else in a bivalved shell, sometimes provided with adductor muscles.

The study of the embryology of some of the higher Crustacea has brought out the fact that in these there are indications of a segment destitute of appendages but represented by a pair of nerve-ganglia, immediately succeeding the eye-bearing anterior segment. In these cases, then, the head really consists altogether of seven segments. Whether this segment represents the first appendage-bearing segment of the lower forms or whether in these also it exists in a degenerate condition has not yet been determined; for convenience at present the six fully-developed head-segments may be considered homologous throughout the group.

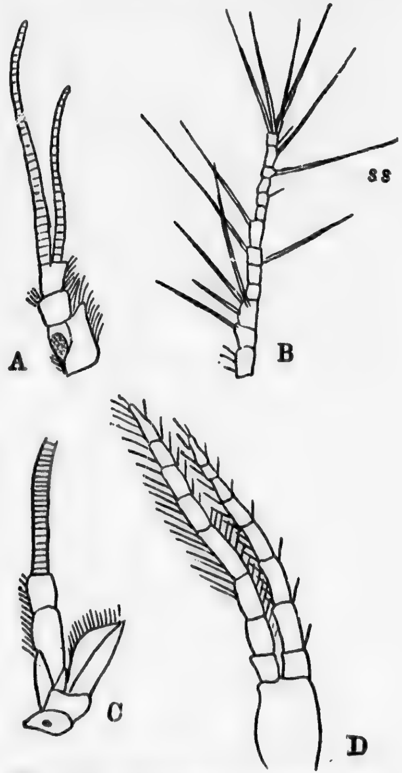

Fig. 168.—Crustacean Appendages.
A, antennule of Crayfish, *Cambarus*; *B*, antennule of Copepod, *Oithona* (after Giesbrecht); *C*, antenna of *Cambarus*; *D*, antenna of Phyllopod, *Eulimnadia* (after Packard); *ss*, sensory hairs.

The appendages vary much in form in different parts of the body and in different forms. Those of the head region are modified to serve as sensory organs and organs of mastication. The first pair, termed the *first antennæ* or *antennules*, are usually sensory in function, though occasionally also locomotor (Ostracoda and some Copepoda), and are frequently supplied with peculiar setæ supposed to be olfactory in addition to others probably tactile in function (Fig. 163, *B*). They consist in their typical form of a basal portion composed of three or four joints, the terminal one bearing one (Fig. 163, *B*) or two (Fig. 163, *A*) many-jointed flagella. The second pair, the *second antennæ* termed also simply *antennæ* (Fig, 163, *C* and *D*), are also principally sensory and consist typically of a two-jointed basal portion, bearing two many-jointed branches. One of these, that upon the outer side, frequently becomes reduced to a scalelike rudiment (Fig. 163, *C*), the inner branch persisting as the flagellum. The third pair, the *mandibles*, serve as masticatory organs and are generally much modified in correspondence with this function. Typically (Fig. 164, *A*) they consist of a two-jointed basal portion bearing two branches. The proximal joint of the basal portion, however, becomes much indurated by the thickening of the chitinous cuticle and also toothed, forming the mandible proper, while the remaining joint and the two branches undergo reduction even to disappearance, being known when present as the *mandibular palps* (Fig. 164, *C*, *mp*). The fourth pair are the *first maxillæ* (Fig. 164, *B* and *D*) and serve like the mandibles for mastication, undergoing a somewhat similar modification. They do not, however, become so indurated, though one or both of the basal joints may be provided with stiff setæ and serve as a jaw, and the two branches more frequently persist than in the mandibles. The fifth pair, the *second maxillæ*, are also masticatory and resemble the first in the modifications which they undergo.

The thoracic and abdominal appendages in all but the lowest forms can be reduced to a typical appendage consisting of a two-jointed basal portion tipped by two branches also jointed. In appendages employed for swimming both branches persist (Fig. 165, *A*), and may possess a broad platelike form, but when modified for walking the outer branch disappears. From limbs modified in this latter

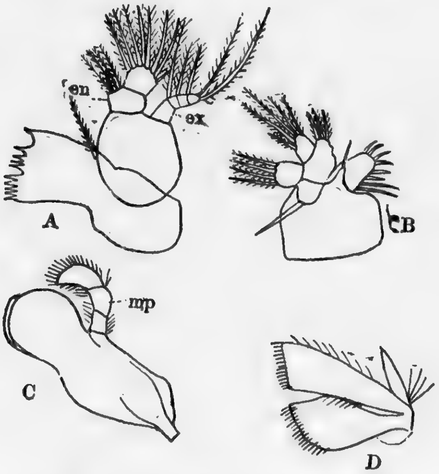

FIG. 164.—CRUSTACEAN APPENDAGES.

A, mandible of Copepod, *Notodelphys* (from BRONN); *B*, first maxilla of *Notodelphys* (from BRONN); *C*, mandible of *Cambarus*; *D*, first maxilla of *Cambarus*.

en = endopodite. *ex* = exopodite. *mp* = mandibular palp.

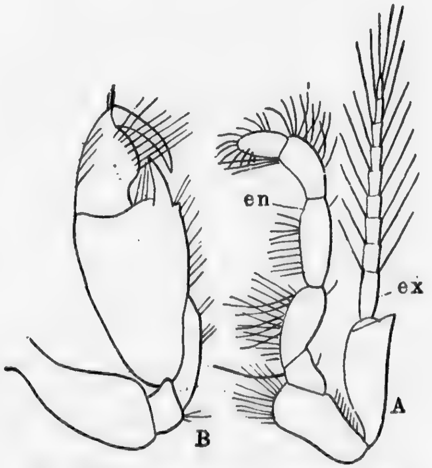

FIG. 165.—CRUSTACEAN APPENDAGES.

A, second thoracic appendage of *Mysis* (after SARS); *B*, second thoracic appendage of an Amphipod.

manner the grasping claws (Fig. 165, *B*) or chelæ are developed by the flexion of the terminal joint on the subterminal or by the elongation of the angles of the latter into a more or less strong process against which the terminal joint may be approximated.

The description given above of the various appendages is of course general, the modifications found in the various forms being almost endless. Indeed in parasitic forms the appendages, except those concerned in mastication, may entirely disappear, all gradations between fully-developed appendages and the merest rudiments being found in various forms.

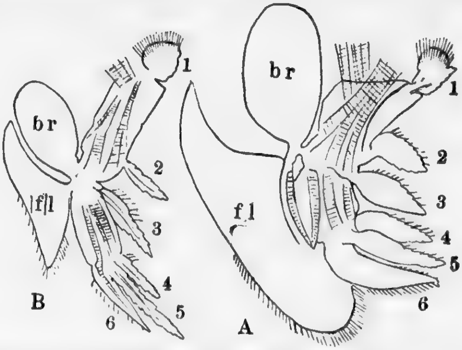

FIG. 166.—SIXTH (*A*) AND SECOND (*B*) THORACIC APPENDAGES OF BRANCHIOPOD, *Apus* (after ZADDACH from BRONN).

br = bract. *fl* = flabellum. 1–6 = inner lobes.

From what has been said, however, it may be seen that typically the Crustacean appendage may be considered a biramous structure, consisting of a two-jointed basal portion termed the *protopodite* and two jointed branches termed the *exopodite* and *endopodite* (Fig. 165, *ex, en*) according to their relation to the median axis of the body. Additional rami are frequently developed upon the protopodite—such, for example, as that termed the *epipodite* (Fig. 167, *ep*) and the branchia (*br*). However, although such a limb may be considered typical, it is not necessarily also the most primitive. Indeed when the simplest forms, such as the Phyllopoda, are examined it will be found that the more posterior appendages have a very different composition. Thus in the genus *Apus* the sixth thoracic appendage (Fig. 166, *A*) consists of a central two-jointed axis ending in a rounded lobe and bearing upon its inner edge six lobes (1–6), some of which are united to the axis by a joint. On the outer side are two large lobes, the distal one being termed the flabellum (*fl*), while the proximal one is the bract (*br*) and serves respiratory purposes. The entire appendage has thus a leaflike form. In one of the more anterior appendages, however, an interesting modification of this will be found. Thus in the second thoracic appendage (Fig. 166, *B*) the axis will be found to be more distinctly divided into two joints, each bearing two of the internal lobes somewhat reduced in size, while the terminal one in addition carries two other lobes, the fifth and sixth, which have become somewhat elongated. The flabellum and bract remain nearly the same as in the first post-genital appendage. If now such an appendage be compared with the second thoracic appendage of the Shrimp *Palæmonetes* (Fig. 167), a direct homology of the parts may be discovered. The axis of the Phyllopod limb is represented by the protopodite while the exopodite (*ex*) and endopodite (*en*) represent the two terminal inner lobes, the others having disappeared; the flabellum is represented by the epipodite (*ep*) and the bract perhaps by the branchia (*br*), attached to the epipodite in this particular limb, but free on the more posterior ones.

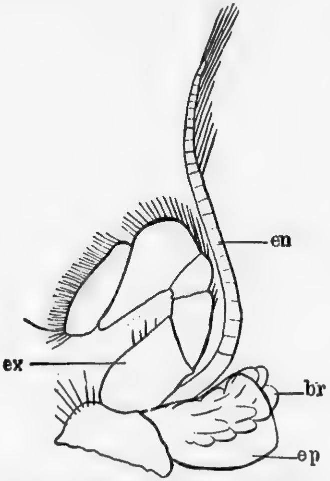

FIG. 167.—THE SECOND MAXILLIPED OF *Palæmonetes*.

br = branchia.
en = endopodite.
ep = epipodite.
ex = exopodite.

It would appear probable from these facts that the biramous limb is really a derivative from the more complicated foliate appendage possessed by the Phyllopods; the foliate condition, however, has given place to such a great extent to the biramous that it is most convenient to regard the latter as the typical condition in the Crustacea.

Respiratory organs are not always present, but when they are they take the form of thin-walled outgrowths of the body-wall. In some forms in which the surface of the body-wall is increased by the development of a bivalved shell or carapace the lining-surface of the fold serves for respiration, and may be thrown into a number of folds so as to increase the extent of surface, as in the Gasteropod *Patella*. In the majority of cases, however, more or less branched hollow processes are seated upon the sides of the body or on a greater or less number of the appendages, their cavities communicating with the lacunar spaces of the body, so that the blood can circulate through them and receive aeration through their thin walls. In the Isopoda a certain number of the appendages are devoted to the respiratory function, both the exopodite and endopodite being lamellar and thin-walled, or else the endopodite alone may have this function, the exopodite serving as a covering-plate for the protection of the inner respiratory ramus.

As already stated, the body is covered by a chitinous or more or less calcareous cuticle. This is secreted by the cells of the hypodermis, as it is termed, which correspond to the ectoderm of other forms and rest below on a more or less well-developed layer of connective tissue. A dermal muscular system is entirely unrepresented in the Crustacea, owing no doubt to the development of the thick cuticula; but nevertheless muscles are well-developed. These take the form in the body of four longitudinal bands, two situated dorsally and two ventrally, giving off slips to be inserted into the cuticle of each metamere, flexion and extension of the various metameres upon one another being thus permitted. In addition muscles extend from the body-wall to the various appendages and between the various joints of these structures, being in all cases, it is needless to say, situated within the body and the appendages. In some cases, more especially in those forms in which the appendages are adapted for walking, special chitinous plates or processes project into the body-cavity from the ventral surface forming the *endophragmal sys-*

tem and serving for the attachment of the muscles passing to the appendages. In forms furnished with a bivalved shell special adductor muscles for its closure are frequently developed; and in the higher Crustacea, in which the so-called stomach is usually provided with a series of chitinous teeth, special muscles are developed for their movement.

The cœlom of the Crustacea consists for the most part of a series of cavities, without definite walls, between the viscera and the muscle-bundles and extending out into the appendages and the branchiæ. One of these occupies the mid-line below the dorsal surface of the body, and contains the heart, whence it is known as the pericardial sinus. It is bounded below by a distinct partition, the pericardial septum, but seems to be a schizocœlic space, since it contains blood, and is therefore not comparable to the pericardial cavity of the Mollusca. A true enterocœl does exist, however, in some of the higher forms (e.g., *Palæmonetes*), consisting of a sac lying in the anterior thoracic region. It surrounds the anterior aorta as a narrow cavity and behind expands so as to cover the anterior portion of the reproductive organs, and then passes ventrally into the schizocœlic cavity which surrounds the intestine. It is a perfectly closed sac, having no communication with the pericardial sinus beneath which it lies, and contains a coagulable fluid in which no corpuscles have been observed.

The saclike cavity into which the antennary gland, to be described later, opens is also to be regarded as a true enterocœl; but attention must again be called to the inadvisability of maintaining a wide distinction between schizocœlic and enterocœlic spaces. (See p. 231.)

The circulatory system is comparatively simple. In many forms a heart and distinct blood-vessels are entirely wanting, the blood circulating through the lacunar cœlom by the movements of the appendages. In the majority of forms, however, a pulsatile heart (Fig. 168, *h*) is present, lying near the dorsal surface of the body in the pericardial sinus, extending in some forms throughout the entire thoracic and abdominal regions of the body. More usually, however, the heart is limited to the thoracic region, or occasionally is almost entirely confined to the abdomen, its anterior extremity encroaching but slightly upon the thorax (Isopoda). It is provided with a varying number of openings along its sides, through which the blood gains entrance to its cavity from the pericardial sinus—these openings, termed *ostia*, being guarded by valves opening inwards and preventing regurgitation of the blood during systole. From either end of the heart arteries arise which, after a longer or shorter course and many or few branchings, open widely into the lacunar spaces. From these the blood passes in some forms into a venous sinus situated on the ventral surface of the body, and thence is distributed to the branchiæ, passing from them back to the pericardial sinus, and so to the heart again. The blood is usually colorless, though occasionally greenish, in which case it contains a respiratory copper-containing pigment termed hæmocyanin, or reddish, in which case the pigment is hæmoglobin. It consists of a plasma in which float amœboid nucleated corpuscles.

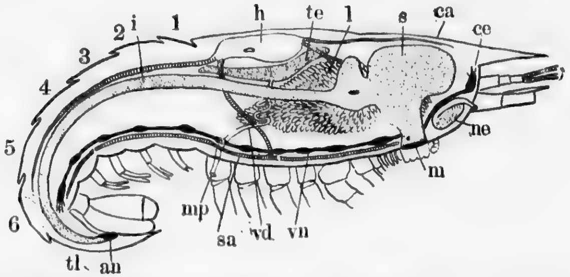

Fig. 168.—Diagram of Structure of Crustacean (*Cambarus*).

an = anus.
ca = carapace.
ce = cerebral ganglion.
h = heart.
i = intestine.
l = digestive gland.
m = mouth.
mp = opening of vas deferens.
ne = nephridium.
s = stomach.
sa = sternal artery.
te = testis.
tl = telson.
vd = vas deferens.
vn = ventral nerve.
1–6 = abdominal segments.

The digestive system consists of an almost straight tube extending from mouth (Fig. 168, *m*) to anus (*an*) and divisible into three regions. The mouth is bounded in front by an overhanging lip, and behind by a lower lip which arises as two separate parts, which by some writers have been regarded as appendages, though the absence of a corresponding nerve-ganglion tells very strongly against such an idea. The anterior portion of the digestive tract arises in the embryo as an ectodermal invagination, and is frequently lined throughout by a chitinous cuticle. In the higher forms (Malacostraca) the posterior portion of this foregut is enlarged to form a so-called stomach (Fig. 168, *s*), in which the chitinous lining thickens to form a complicated arrangement of teeth, which, moved by special muscles extending from the stomach to the walls of the body, serve for the comminution of the food. No salivary glands occur. The midgut is frequently of very small extent, and has usually connected with it a digestive gland (Fig. 168, *l*) consisting either of from one to four pairs of simple or but slightly branched cœcal tubes, or else of a much-branched compact gland opening into the intestine by two or more ducts. The hindgut (*i*), like the foregut, arises as an ectodermal invagination, and is usually lined with chitin and unprovided with special glands.

The nervous system presents a typically metameric condition throughout the greater portion of the body, a pair of ganglia occurring in each segment, united by paired connectives with the ganglia of the preceding and succeeding metameres (Fig. 168, *vn*). In the anterior portion of the body, however, as well as posteriorly, a certain amount of concentration and fusion of the various ganglia occurs. An ideal condition in which no fusion has taken place would show a pair of cerebral ganglia (Fig. 169, *ce*) with which more or less complicated optic ganglia are connected. From the cerebral ganglia connectives pass backward and unite with a pair of ganglia (g^1), clearly indicated in the embryos of many of the higher forms, but not yet definitely known in the Entomostraca, though it seems probable that they occur in these also. The metamere and appendages which should properly be associated with them seem to have disappeared; that is to say, they are the sole representatives of a metamere intervening between the cerebral and antennulary segments. These ganglia are united by a pair of connectives with a third pair sending nerves to the antennules (g^2), and these again with a fourth pair belonging to the antennary metamere (g^3), and so on, a pair of ganglia occurring in each metamere throughout the body. Such a condition as this is found only in embryonic stages, and even there not always perfectly. The ganglia representing the preantennulary metamere fuse with the cerebral, as do also the antennulary, and in higher forms the antennary ganglia, there being thus formed a complex cerebrum, which, in contrast to the simple cerebrum (*archicerebrum*) of the Annelida, may be known as a *syncerebrum.* The remaining ganglia may remain perfectly separate, the connectives joining the more anterior ones usually being much shortened, or a greater or less number of them may fuse. Thus in the Crayfish the ganglia of the three posterior

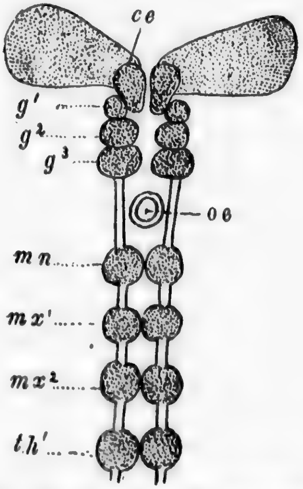

Fig. 169.—Diagram of Nervous System of Crustacean.
ce = cerebral ganglion.
g^1 = second "
g^2 = antennulary "
g^3 = antennary "
mn = mandibular "
mx^1, mx^2 = maxillary ganglia.
œ = œsophagus.
th^1 = first thoracic ganglion.

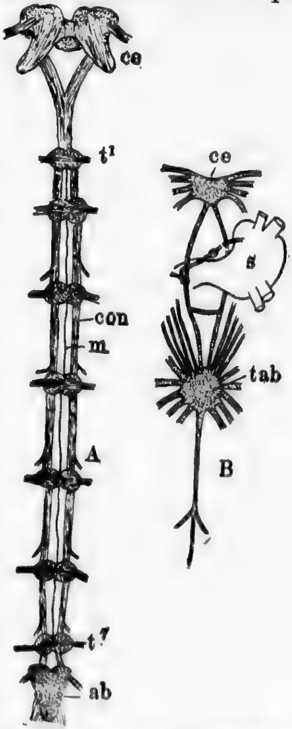

Fig. 170.—Nervous System of (*A*) an Isopod, *Asellus*, and (*B*) a Brachyuran Decapod, *Maja* (after Milne-Edwards).

head-metameres unite with those of the two anterior thoracic segments to form a single ganglionic mass lying behind the œsophagus and sending nerves to the appendages of the somites represented in the fusion. Similarly, in the posterior region of the body of the Isopoda all the ganglia of the abdominal region may fuse to a more or less simple mass (Fig. 170, *A*, *ab*), and an extreme condition of fusion is to be found in some Crabs (Fig. 170, *B*), in which all the ganglia behind the antennary segment fuse to a single mass (*tab*), lying in the thorax—a condition standing in relation to the reduction of the abdomen and the extensive concentration of the head and thoracic regions which are characteristic of these forms.

A sympathetic nervous system seems to be generally present, consisting in its most complete condition of an unpaired nerve arising from the syncerebrum and passing backwards to be distributed to the stomach, and of a median nerve (Fig. 170, *A*, *m*) extending from one pair of postœsophageal ganglia to the other, lying between the two connectives.

Sense-organs reach a high degree of development in the group. Hairs occur in abundance on the appendages and body, the majority no doubt having merely a mechanical function; but among them will be found some beneath which lie one or more ganglion-cells, giving rise to a nerve which passes into the hair. These hairs are supposed to be tactile in function. On the antennules of many forms and more rarely upon the antennæ, hairs of special forms occur, usually in bunches or in rows. They may be club-shaped or cylindrical, and each has a nerve-fibre extending into it without dilating into a ganglion-cell beneath its base. To these hairs an olfactory function has been assigned, and it is noticeable that they are usually more abundant upon the antennules of the males than on those of the females—an arrangement which suggests a probable service as guides in finding the latter.

Eyes are very generally present in the Crustacea, and reach usually a high degree of efficiency. Two forms of eye are known—a median unpaired one, frequently spoken of as the simple eye, and the lateral or compound eyes. The unpaired eye is present in the larval stages of probably all Crustacea, and persists in a more or less perfect form in the adults of most Entomostraca,—a group which contains the more primitive forms,—and has even been detected in those of some of the higher forms (e.g. *Crangon*). It consists when well developed of three patches of pigment, forming cups in each of which lies a group of clear cells from which nerve-fibres arise passing to the optic nerve.

The lateral eyes are composed of a number of units each of which possesses all the parts of a visual organ and is termed an *ommatidium*, and consequently these eyes have been regarded as an aggregation of a number of individual eyes, whence the term compound usually applied to them. Each ommatidium is a complicated structure consisting of several parts (Fig. 171). The outermost layer of each is a transparent cornea which is continuous with the general cuticle of the body, and in some forms is only distinguished from this by its transparency. More frequently, however, this cuticle becomes more or less perfectly divided into a series of corneas of an hexagonal or tetragonal shape, one corresponding to each ommatidium, the surface of the eye thus acquiring a faceted appearance. Below the cuticle come the hypodermal cells (*CH*) which secrete it, arranged irregularly without reference to the ommatidia in the simpler non-faceted eyes, but in the faceted eyes with two hypodermal cells lying beneath each cornea and constituting the corneal hypodermis. Below these come the cone cells (*C*), two to four in number as a rule; these are elongated cells a portion of whose protoplasm becomes converted into a refractive translucent body, the crystalline cone (*CC*), composed of as many segments as there are cone-cells taking part in its formation, and sur-

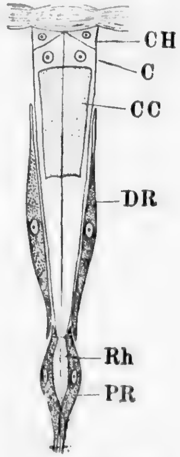

FIG. 171. — DIAGRAM OF CRUSTACEAN OMMATIDIUM.

C = cone-cell.
CH = corneal hypodermis.
CC = crystalline cone.
DR = distal retinula.
PR = proximal retinula.
Rh = rhabdom.

rounded upon the outside by a delicate layer of protoplasm placing the part of each cell above the cone in continuity with the part lying below it. In the higher forms there occur, partially surrounding the cone-cells, two pigmented cells which seem to be sensory in function and are termed the distal retinular cells (*DR*). They are, however, unrepresented in the lower forms, in which the sensory portion or retinula is represented by a single circle of usually 5 cells (*PR*) lying proximally to the cone-cells and surrounding a chitinous rod which is manufactured as a secretion from their approximated surfaces, and is termed the rhabdom (*Rh*). These cells are also pigmented and are prolonged below into nerve-fibres, which, piercing the basement-membrane upon which the ommatidia rest, pass to the optic ganglia. In the higher Crustacea, in which a distal retinula is present, the rhabdom is formed by a circle of eight cells (one of which is almost aborted, so that there appear to be only seven). These constitute the proximal retinula, and appear to correspond to the single retinula of the simpler forms. Finally, a number of accessory cells, usually pigmented, may surround each ommatidium, separating it from its neighbors, but not appearing to be essential constituents of the eye.

The view according to which these lateral eyes are regarded as an aggregation of a number of independent eyes has already been referred to. It seems questionable, however, if this be the correct interpretation of them in view of the occurrence of so-called compound eyes in the Mollusca (*Arca*) and the Polychætous Annelida. It seems more probable that, as in these forms, the Crustacean eye is to be regarded as a separation into a number of more or less isolated parts of an originally continuous retina, a corresponding division of the originally simple refractive apparatus also taking place. This view seems to harmonize most satisfactorily with the facts of development.

Occasional departures from the usual arrangement of the eyes are to be found—as for instance in *Phronima*, one of the Amphipoda, in which two pairs of compound eyes occur on the head. Mention may also be made here of the peculiar eyelike structures occurring in *Euphausia*, one of the Schizopoda. They occur on the basal joints of the appendages of certain of the thoracic metameres, as well as upon the ventral surface of the abdomen, and appear to be rather phosphorescent than optic organs.

Otocysts occur throughout the group Decapoda, to which the Crayfish, Lobster, and Crab belong, and consist of sacs lined by sensory setæ and containing otoliths. They are situated on the basal joint of each of the antennules and in some forms are completely closed, though usually their cavity communicates with the exterior, being guarded by a number of closely-approximated bristles. In the Schizopoda similar otocysts occur in the endopodite of the last pair of abdominal appendages, and in the Amphipod *Oxycephalus* two lie above the syncerebrum. These structures, which are usually spoken of as auditory organs, seem to be rather sense-organs of equilibrium.

In the larvæ of many forms and in the adults of some Entomostraca one or two papilla-like processes project from the anterior surface of the head and are supposed to be sensory in function, though what purpose they may subserve is unknown. Strong nerves pass to these frontal sense-organs which appear to be of considerable importance.

The excretory system consists of two pairs of nephridia, one or other of which may be absent in many forms. One of these develops in connection with the antennary segment and opens to the exterior on the basal joint of the antennæ (Fig. 168, *ne*), whence it is known as the antennary gland, sometimes, however, receiving the name of the green gland. It reaches its highest development among the Malacostraca, occurring in many Entomostraca only in larval stages, later on degenerating. In its simplest condition it consists of a coiled tube whose lumen appears in some cases to be intracellular, though in others it is undoubtedly intercellular, and which terminates internally in a saclike dilatation whose wall is richly supplied with blood-lacunæ. In the higher forms (Fig. 172, *A*) a great complexity is brought about by the development of lateral branches from the tubular portion, and the terminal sac (*s*) may enlarge and fuse with that of the opposite side to form a cavity of considerable size lying in the anterior portion of the thorax and termed the nephroperitoneal sac.

The second nephridium (Fig. 172, *B*) develops in connection with the second maxillary segment, and opens usually upon the appendage of that segment. It is especially developed in the Entomostraca, in which it may lie in the folds of the body-wall which form the shell, and hence is usually known as the shell-gland. It occurs also in the larval stages of many Malacostraca, and may possibly persist in a degenerated condition in the adults of some forms. In structure it resembles closely the antennary gland, but does not present the complexity frequently found in that gland.

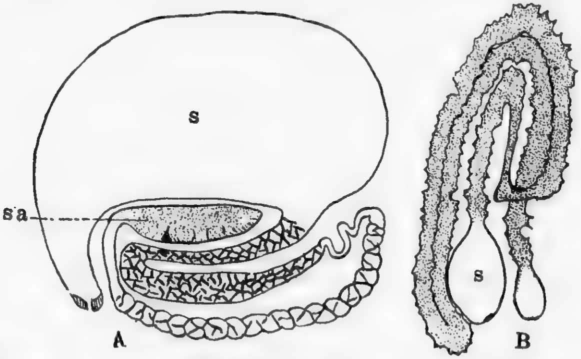

FIG. 172.—*A*, DIAGRAM OF NEPHRIDIUM (GREEN-GLAND) OF *Astacus* (after MARCHAL); *B*, SHELL-GLAND OF *Eulimnadia*.
s = terminal sac. *sa* = saccule.

The majority of the Crustacea are bisexual, hermaphroditism occurring only in forms which have a parasitic habit and in some which are sessile in adult life (Cirrhipedia). The ovaries or testes (Figs. 173, *A* and *B*) are paired organs lying alongside of the intestine or slightly dorsal to that organ, transverse connecting bars in some cases passing from the organ of one side to that of the other. Each organ may be regarded as a tube, sometimes simple, sometimes branched, and lined on its interior by an epithelium which gives rise to the germ-cells. Special germ-producing regions are frequently developed, as, for instance, at the extremities of the tubes or along one side (Isopoda), the cells in other regions ceasing to give rise to ova or spermatozoa. The reproductive elements pass to the exterior by special ducts, oviducts (*od*) or vasa deferentia (*vd*), connected with each organ, and opening usually upon the ventral surface of the body at or near the junction of the thoracic and abdominal regions. The origin of these ducts has not yet been discovered, but it has been suggested that they may represent a third pair of nephridia. Accessory structures, such as receptacula seminis and cement-glands, for the attachment of the ova in the females, and spermatophore-sacs, in which the spermatozoa are encapsuled in spermatophores in the males, are frequently developed in connection with the ducts, and in the Malacostraca certain of the appendages in the neighborhood of the genital openings are, especially in the males, modified so as to serve as copulatory organs.

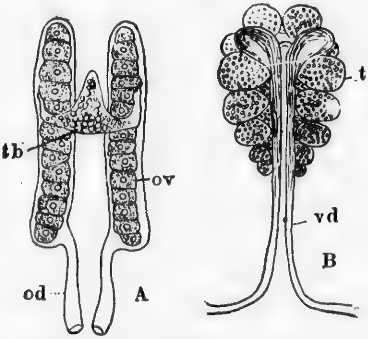

FIG. 173.—*A*, OVARY, AND *B*, TESTIS OF *Mysis* (after SARS).

od = oviduct.
ov = ovary.
tb = transverse bar of ovary.
te = testis.
vd = vas deferens.

Owing to the great variety of form and structure met with in the various species of Crustacea the group is separable into a large number of subdivisions. Two principal classes are, however, readily discernible, of which the first is

I. CLASS **Entomostraca.**

In this class the number of segments of which the body is composed varies greatly in the various groups and even in closely-related genera. The abdominal region is in some forms very much abreviated and is destitute of appendages, a rule which, however, finds exception in certain Phyllopods in which some of the segments behind the genital openings, which may be taken as indicating the line of separation between the two regions, are provided with appendages. Folds arising from the head region and forming either a carapace or a bivalved shell are frequently present and the animals are for the most part small, the largest reaching a length of about eight centimetres, while the majority measure less than a millimetre. The unpaired eye usually persists in the adult, as does also the shell-gland, the antennary gland, on the other hand, being usually rudimentary or absent. A masticatory stomach is never present, and a further characteristic is found in the fact that the larva which hatches from the egg is almost invariably a Nauplius (see p. 417).

1. Order **Phyllopoda.**

The Phyllopoda are principally confined to fresh water, the genus *Artemia*, however, being found in salt lakes, while a few Cladocera are marine. They seem to be the most primitive of all the Crustacea and present the greatest variation in the number of metameres composing the body, some species possessing over forty pairs of appendages, while in others again the number is reduced to nine. All the thoracic appendages, however, as a rule bear branchial lobes, and in some cases (*Apus*) present the many-lobed and imperfectly-jointed condition which has been considered the most primitive form of the Crustacean limb (see p. 373). The antennules are usually small and abundantly provided with olfactory hairs, while the antennæ (except in *Apus*, in which they entirely disappear) are long and serve as locomotor organs. The mandibles are reduced to simple masticatory plates without palps, and the maxillæ undergo likewise considerable reduction. A heart is always present, but no blood-vessels exist, the blood passing from the heart into lacunar spaces.

1. Suborder *Branchiopoda.*

The Branchiopoda have all a plainly-segmented body consisting of many segments, and, with the exception of *Branchipus* and *Artemia*, are provided with a fold of the body-wall which may form a dorsal carapace, as in *Apus*, or a bivalved shell, as in *Limnadia*, *Limnetis*, and *Estheria* (Fig. 174), an adductor muscle being developed for the closure of the shell within which the entire body may be withdrawn. The antennules are as a rule small and are provided with olfactory hairs; the antennæ, on the other hand, are well developed except in *Apus*, in which they are in some species quite small and in others entirely wanting. In the shelled forms they are biramous, consisting of a several-jointed protopodite terminated by two many-jointed flagella, and serve as oarlike locomotor organs, but in *Branchipus* they are short strong structures without any locomotor function, serving in the males as clasping organs of use in copulation. The mandibles are reduced to toothed plates, lacking a palp, and the first maxillæ show an almost similar reduction, while the second are entirely wanting in some genera, such as *Limnetis*. The succeeding appendages are not limited to the thoracic region of the body, taking the genital opening as the limit between the two regions. Thus in *Apus cancriformis* there are eleven thoracic appendages, while behind the genital ring there are no less than over fifty locomotor limbs, and in such forms as *Limnetis* and *Estheria* (Fig. 174) it is difficult to distinguish between the thorax and the anterior abdominal segments.

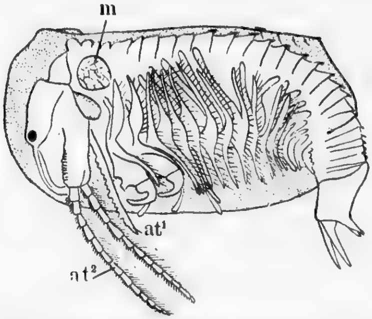

FIG. 174.—*Estheria compleximanus* (after PACKARD).
at^1 = antennule. *at*^{2} = antenna. *m* = shell-muscle.

The heart of the Branchiopoda is a more or less elongated organ with several ostia and is usually limited to the anterior portion of the thoracic cavity, though in *Branchipus* it extends into the anterior abdominal region. Lateral eyes are present in addition to the unpaired median eye. In *Branchipus* they are situated upon the sides of the head upon well-defined stalks, but in *Apus* they are closely approximated on the dorsal surface of the cephalo-thoracic carapace, while in the shelled forms they are united together to form a single eye whose double nature is revealed only by a study of the details in its arrangement.

A peculiar feature in the life-history of the members of this group is the comparative infrequency of males, their proportion to females being so small that for some time they were not known to exist. The females are able to reproduce parthenogenetically—males appearing only under certain conditions which are not as yet satisfactorily understood. The eggs develop generally in brood-pouches situated upon certain of the thoracic appendages (*Apus*, *Limnadia*) or else are affixed to filamentar processes of these appendages (*Estheria*).

2. Suborder *Cladocera*.

The Cladocera are distinguished from the Branchiopoda by the segmentation of the body being much less clearly defined and by the small and more definite number of appendages, there being only from four to six pairs of thoracic limbs. A bivalved shell arising from the maxillary segments and provided with an adductor muscle is always present; it does not enclose the head, but the rest of the body may be completely withdrawn within it except in some genera, such as *Evadne* and *Polyphemus*, in which it is transformed into a brood-chamber, leaving the body almost unprotected.

The antennules are always small unjointed structures provided with a bunch of olfactory hairs usually terminal in position, and the antennæ are strong biramous locomotor organs. The mandibles are simple toothed plates without palps, and the second maxillæ are usually entirely wanting in the adults. The thoracic limbs are six in number in the genus *Sida* and are all lamellate and abundantly supplied with marginal setæ, but in *Daphnia* (Fig. 175), *Moina*, and allied forms the number is reduced to five, and the more anterior ones are more or less modified towards simple cylindrical jointed appendages, a condition found in all the four thoracic appendages of *Evadne*

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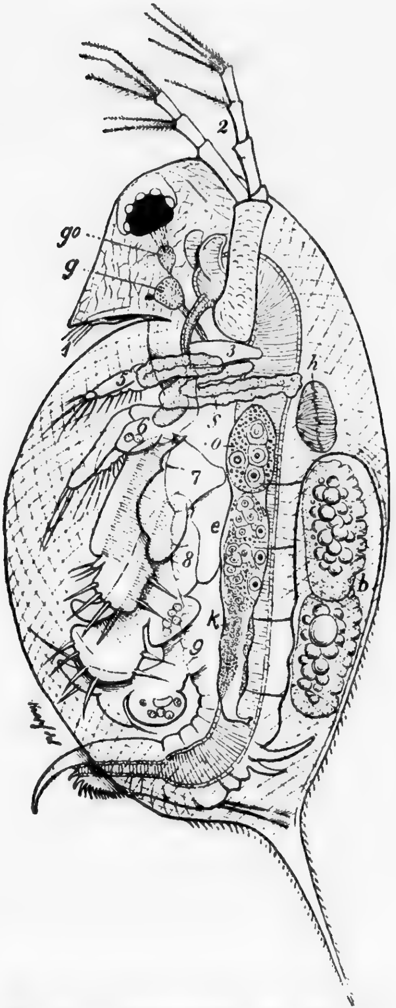

FIG. 175.—*Daphnia pulex* (from HERTWIG).

b = brood-pouch.
e = immature ova.
g = cerebral ganglion.
go = optic ganglion.
h = heart.
k = germinal region of ovary.
o = ovary.
s = shell gland.
1 = antennule.
2 = antenna.
3 = mandible.
5–9 = thoracic limbs.

and *Polyphemus*, the branchial lobes being at the same time rudimentary or entirely wanting. The abdomen, which is composed of four segments, possesses on its dorsal surface elevations for the closure behind of the brood-chamber, and on its terminal segment setæ are usually developed; it does not, however, bear any appendages.

The heart is an oval structure situated in the thoracic region and possesses but a single pair of ostia. The lateral eyes are in all cases fused to form a double eye situated in the median line of the head and capable of movement within a socket by means of muscles which are attached to it.

The majority of the Cladocera are fresh-water forms, though some, such as *Evadne*, are marine. The ova undergo development in a brood-chamber formed by the space included between the shell-valves and the dorsal surface of the abdomen, and in *Evadne* and *Polyphemus*, as already stated, the entire shell, which is somewhat reduced in size, is adapted to serve as walls for the chamber.

As in the Branchiopoda, collections of Cladocera, especially if made during the spring or summer, will show an enormous preponderance of females, and several generations may be reared without a single male making its appearance. The eggs, which have a thin egg-membrane and little yolk, develop parthenogenetically and produce females, and this method of reproduction will continue so long as the conditions, such as temperature and food, remain satisfactory; hence the eggs of this kind are generally known as "summer eggs." Towards autumn, however, or whenever the conditions tend to become unfavorable, males, distinguishable by their smaller size, the absence of a brood-pouch, and their more highly-developed sense-organs, as well as by the development of hooked setæ on the anterior appendages which serve as clasping organs, make their appearance, and at the same time the females begin to deposit ova much larger in size than the summer eggs and containing a considerable amount of yolk. These "winter eggs" develop apparently only after fertilization. In *Polyphemus* they possess a thick shell, but in other forms special arrangements occur to render them resistent to cold, drying, etc. In some forms the maternal shell is sloughed and serves as a protecting case, but more usually, as in *Daphnia*, *Moina*, and others, a saddle-shaped thickening, the *ephippium*, appears on the dorsal wall of the brood-pouch at the time of the passage of the winter egg into it, and this thickening is thrown off with the egg and forms a protective covering for it.

2. Order **Ostracoda.**

The Ostracoda resemble the Cladocera in the segmentation of the body being but slightly marked and in possessing a bivalved shell provided with an adductor muscle. The shell, however, encloses the head as well as the thoracic and abdominal regions, and furthermore but two thoracic limbs exist.

The antennules and antennæ are both uniramous appendages and serve for creeping, though the former are also provided with olfactory hairs. The mandible consists of a tooth-bearing plate and a strong jointed palp which in some forms also functions as a creeping limb, and behind it are two well-developed maxillæ. The first of these is distinguished by the development of the jaw portion and the reduction of the palp, and in *Cypris* and *Cythere* bears a large plate with numerous marginal setæ which is usually termed a branchial lobe. The second maxilla, on the other hand, shows considerable modification in different genera. In *Cypridina* (Fig. 176, *Mx^2*) it is jawlike and bears a large branchial lobe (wanting on the first pair), and in *Cypris* is adapted for the same function, but bears in addition to the rudimentary branchial lobe a short two-jointed palp, which in *Halocypris* becomes enlarged to form a three- or four-jointed limb, while finally in *Cythere* the appendage is practically a walking limb, its jaw function not being developed. The first thoracic appendage is an elongated many-jointed limb except in *Cypridina* (Fig. 176, *t'*), where it possesses a jaw function, and the second is also limblike. In *Halocypris* this latter appendage is, however, rudimentary, and in *Cypris* and *Cypridina* (Fig. 176, *T^2*) it is dorsally directed and serves for cleansing the inner surface of the shell from foreign bodies, in the latter genus arising some distance up upon the sides of the body and forming a long cylindrical unjointed appendage.

Respiration is usually effected by the general surface of the body and the inner walls of the shell duplicature, though in certain Cypridinidæ a double row of respiratory processes are situated upon the dorsal surface of the body near the second thoracic appendage. The so-called branchial lobes on the maxillæ probably subserve the respiratory function only by renewing the water in contact with the body surface. A single median eye alone is present in *Cypris* and *Cythere*, but in addition a pair of lateral compound eyes occurs in *Cypridina*. The frontal sense-organ is a single strong process, in certain forms lying slightly above and between the antennules. A heart is present in *Cypridina* and *Halocypris* as a saclike organ with two lateral ostia and is not prolonged into arteries. In *Cypris* and *Cythere* it is entirely wanting.

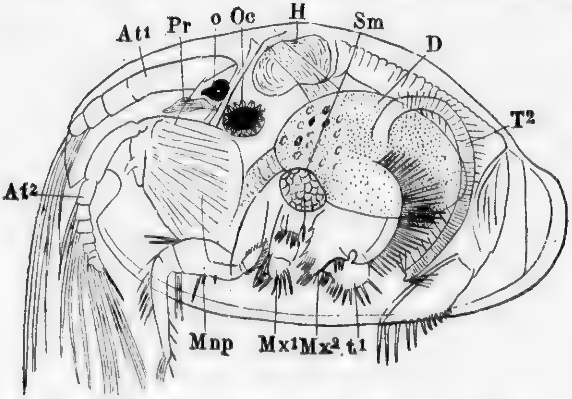

FIG. 176.—*Cypridina mediterranea*, FEMALE (after CLAUS).

At^1 = antennule.
At^2 = antenna.
h = heart.
Mnp = mandibular palp.
Mx^1, Mx^2 = first and second maxilla.
o = simple eye.
Oc = compound eye.
Pr = frontal organ.
Sm = shell-muscle.
t^1, T^2 = first and second thoracic appendages.

The Ostracoda occur both in fresh water and in the ocean. The genus *Cypris* and its allies are for the most part aquatic, while the other genera mentioned are exclusively marine.

3. Order **Copepoda.**

The members of the order Copepoda present great variations in form, due to the fact that there are a number of parasitic forms belonging to it some of which show so much degeneration that their relationships to the non-parasitic forms only become apparent by a study of their development. Typically, however, the body is generally elongated (Fig. 177) and consists of ten segments in addition to those of the head, the five anterior ones usually bearing appendages and constituting the thorax, while the five posterior lack appendages and form the abdomen, the terminal segment of which bears a pair of caudal furcæ provided with setæ. In female individuals the two anterior abdominal segments fuse together to form a genital double segment, and in all cases the head segments fuse together, while the anterior thoracic segment usually fuses with this consolidated mass. No shell-duplicature occurs. In the parasitic forms there is a tendency for the various segments to become indistinct and all trace of them may vanish, the abdomen in some cases becoming also extremely reduced in size. Add to this that lobes and processes are frequently developed upon the body and it will be understood how far these degenerate forms depart from the typical arrangement.

The antennules (Fig. 177, *at*^{1}) in all free-swimming Copepoda form long many-jointed swimming-organs used in an oarlike manner. They consist of a certain number of stout basal joints, terminated by a single long multiarticulate flagellum, no trace of a biramous condition being apparent. In addition to their locomotor function they also, as in other forms, serve as sense-organs, olfactory hairs being scattered along the flagellum, and in male individuals they are specially modified to form clasping organs for use in copulation. The antennæ (*at*^{2}) are much smaller and are frequently biramous, and the mandible (*mn*) has usually a palp, while the first maxillæ (*mx*^{1}), bearing strong masticatory bristles on their basal joints, also show more or less indication of a biramous condition. The second maxillæ (*mx*^{2}), sometimes termed the maxillipeds, have generally been regarded as representing a single pair of appendages whose exopodites and endopodites have separated from each other. It is now known, however, that they really represent two pairs of appendages which have lost their exopodites and have been approximated. The anterior pair are small plates provided with numerous masticatory setæ on their inner edges, and are the true second maxillæ, while the posterior pair, elongated and limblike, are really thoracic limbs and so may be termed maxillipeds. The other thoracic appendages (t^1–t^5) are typically biramous and serve for swimming.

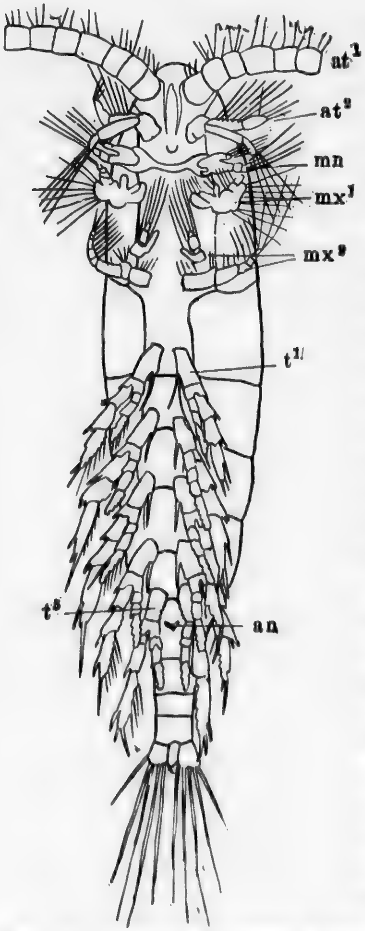

Fig. 177.—*Calanus hyperboreus* (after Giesbrecht).

an = anus.
at^1 = antennule.
at^2 = antenna.
mn = mandible.
mx^1, *mx*^{2} = first and second maxillæ.
t^1–t^5 = thoracic appendages.

This description refers to the free-swimming forms; in parasitic species much modification of the appendages ensues. The antennules lose their long oarlike character and may even be degenerated to strong hooks which serve to fasten the animal to its host, a degeneration which the antennæ may also undergo. The mouth-parts become adapted to a piercing function, and the mandibles are represented by sharp styletlike structures, sometimes enclosed in a tube formed by the union of the upper and lower lips, a sucking-organ being thus produced. The first maxillæ undergo considerable reduction, while the second pair is frequently adapted to form organs for adhering to the host, and finally the thoracic appendages may undergo various stages of degeneration, in some forms entirely disappearing.

Branchial organs are entirely wanting throughout the order, respiration taking place over the entire body surface. A heart is present in a few forms (Calanidæ) consisting of a saclike organ with but a single pair of ostia, but in the majority of cases it is wanting. A single median eye is generally present, and in a few forms, *Pontella*, *Corycœus*, and *Argulus*, lateral eyes are also present, though absent as a rule throughout the group. Each lateral eye in *Corycœus* consists of a single ommatidium, but in *Argulus* is compound and similar to the lateral eyes of the Branchiopoda.

The Copepoda are throughout bisexual even in the cases of the parasitic forms. The vasa deferentia are provided with an enlargement in which the spermatozoa are included within a capsule, forming a spermatophore which during copulation is deposited in the neighborhood of the female genital opening. The spermatozoa being discharged from the spermatophore-capsule, by a special discharging apparatus with which it is provided, make their way into a receptaculum seminis which communicates with each oviduct, the ova being fertilized during their passage to the exterior. These are usually carried in one or two masses attached to the first abdominal segment of the female, though in some forms, such as *Notodelphys*, they undergo their development in a brood-chamber formed by the duplication of the integument of the dorsal surfaces of the fourth and fifth thoracic segments. A peculiar dimorphism of the sexes occurs in some of the most highly modified parasites, such as *Chondracanthus*, *Achtheres*, and others, the male being very much smaller than the female and showing much less degradation, frequently presenting well-developed eyes and more or less perfectly-developed appendages, so that it is able to lead for a time a free existence. It is to be regarded as a larval stage sexually mature, since it resembles closely the female when in the stage immediately before fixation to its host, the greater part of the degeneration taking place after that has been accomplished.

Two suborders are recognizable.

1. Suborder *Eucopepoda.*

This suborder includes the majority of the Copepoda, and its members are characterized by having only the first thoracic segment fused with the head and by possessing usually a well-developed abdomen. Many are free-swimming, some inhabiting fresh water, as *Cyclops* and *Canthocamptus*, while others are more especially marine, such as *Harpacticus*, *Calanus* (Fig. 177), and *Cetochilus*, the latter sometimes occurring in enormous schools, and forming an important food-supply for fish and the baleen whales. Some, on the other hand, lead a commensalistic life, occurring in the branchial chamber of Tunicates, e.g. *Notodelphys*, while a large number of forms are parasitic. The degree of parasitism varies greatly in different forms; thus many are capable of free existence, becoming parasitic only occasionally, such as *Corycæus* and the brilliantly-colored *Sapphirina*, while others, such as *Ergasilus*, parasitic on the gills of fishes, and *Caligus* and *Pandarus*, though essen-

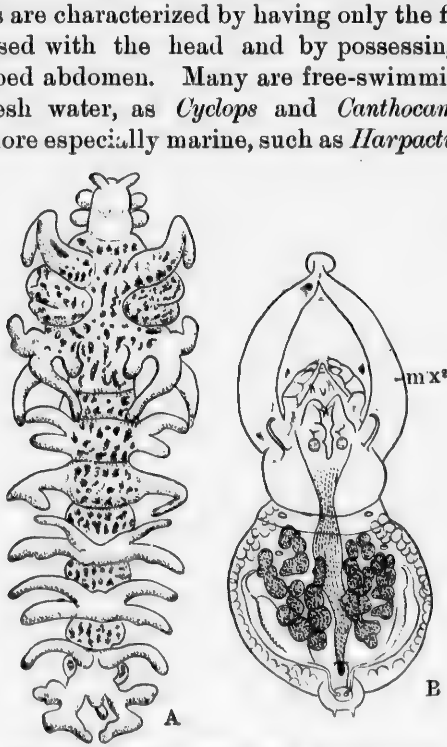

FIG. 178.—*A*, *Philichthys xiphiæ* SEEN FROM THE DORSAL SURFACE (after CLAUS); *B*, *Achtheres percarum* (from BRONN).

tially parasitic, still retain more or less perfectly the segmentation and general appearance of free-swimming forms, the modifications which they have undergone affecting principally the antennæ, which are modified for purposes of adhesion to the host, the mandibles, which are piercing organs, and in some cases the maxillæ, which may, like the antennæ, become hook-like. Frequently, however, the body assumes aberrant forms, as in *Philichthys* (Fig. 178, *A*), and the segmentation may entirely disappear, as in *Penella, Lernœa, Chondracanthus, Achtheres* (Fig. 178, *B*), and *Anchorella,* these last two forms presenting a peculiar modification of the second maxillæ in the females, the two appendages fusing at their tips to form a chitinous adhesive disk which serves as an organ of adhesion. In the majority of these forms, as already noted, the thoracic appendages may become more or less rudimentary; indeed even in the less modified forms, such as *Ergasilus*, the appendages of the fifth thoracic segment may be wanting.

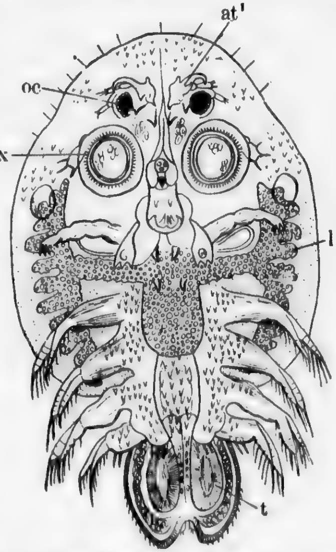

FIG. 179.—***Argulus foliaceus*** **(after CLAUS).**
at' = antennules.
l = digestive gland.
mx = second maxilla.
oc = eye.
t = testis.

2. Suborder *Branchiura.*

In the Branchiura the cephalic and thoracic segments are fused together to form a shield-shaped cephalothorax, while the abdomen is small and divided into two platelike halves which have a rich blood-supply, apparently serving respiratory purposes, and in the males contain the testes.

The basal joint of the antennules (Fig. 179, *at'*) is developed into a strong hooked process, and the mandibles and first maxillæ, which are stylet-like, are enclosed in a tube formed by the fusion of the upper and lower lips. The second maxillæ (*mx*) develop at their bases large suckers, while the first thoracic appendages, here termed maxillipeds, are limblike and have also hooked processes upon the basal joints. These are succeeded by four pairs of biramous swimming appendages.

A well-developed heart is present, giving rise to arteries extending throughout the length of the body. A pair of lateral compound eyes (*oc*) are also present, and a further difference from the majority of the Eucopepoda lies in the fact that the eggs are not carried by the female, but are deposited on foreign bodies.

All the forms are parasitic, in some cases, as *Argulus*, upon fresh-water fishes, but they also possess the power of swimming actively.

4. Order **Cirrhipedia.**

The Cirrhipedia or Barnacles are without exception marine forms, and in the adult condition either adhere to foreign bodies, leading a perfectly sessile life, or else bore in the shells of certain Mollusca, or finally are parasitic. It will be convenient to describe first of all the organization of the sessile and boring forms, later considering briefly the parasitic forms which show many peculiarities due to degeneration.

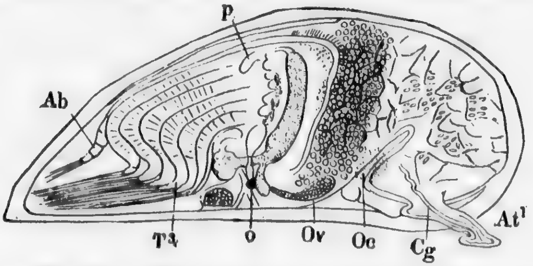

FIG. 180.—CYPRIS LARVA OF *Lepas* (after CLAUS).

Ab = abdomen.
At^1 = antennules.
Cg = duct of cement-gland.
o = opening of oviduct.
Oc = eye.
Ov = ovary.
p = penis.
T^3 = third thoracic foot.

During the course of development the Cirrhipedia all pass through a larval stage similar in general appearance to an

Ostracode and hence termed the Cypris-stage (Fig. 180). The body is enclosed in extensive folds of the body-wall termed the mantle, and the antennules (at^1) are characterized by being directed forwards and terminating in an adhesive disk upon which open the ducts of cement-glands. Adhering to a foreign body by these disks, the adhesion being made permanent by the secretion of the glands, a rotation of the body upon the antennæ through 90° takes place, so that the animal comes to lie upon its back, the ventral surface looking away from the point of fixation. The antennules persist as rudimentary structures, and the adult animal really seems to be fixed by the dorsal surface of the head, which may elongate to form a stalk bearing the body proper at its extremity (*Lepas*, Fig. 181).

The body shows no indication of segmentation, but a head region may be distinguished from the thorax and this from a short abdomen by means of the appendages. The character of the antennules has already been mentioned; the antennæ are wanting in adults, and the mandibles and first maxillæ are simple toothed plates destitute of palps, while the second maxillæ are small and fused together to form a kind of lower lip. The thoracic appendages (Fig. 181, *B*) are biramous, the basal portion supporting two long multiarticulate and usually setose filaments. In typical cases six pairs of these appendages occur, but they may be reduced to four (*Alcippe*) or three pairs (*Cryptophialus*). In the living animal flexions of these appendages towards the ventral surface of the body take place almost rhythmically, currents of water being thus impelled towards the mouth together with any food-particles they may contain. The abdomen does not bear appendages, but from it arises a long slender cirrus (Fig. 181, *B, cir*) which contains the terminal portions of the vasa deferentia.

The mantle-folds which occur in the Cypris-larva persist in the adult, and calcification of their walls takes place, giving rise to a calcareous shell, composed of several pieces, which encloses the animal. In the genus *Lepas*, the goose-barnacle, this shell consists of five pieces. On the dorsal side there is a single unpaired piece which receives the name of the *carina* (Fig. 181, *A, car*); at the sides and resting below on the uppermost part of the stalk are the two *scuta* (*sc*), while above these are the *terga* (*te*), also paired, the opening into the interior lying between the terga and the scuta of opposite sides. In *Scalpellum* between the two scuta a sixth, unpaired, piece, the *rostrum*, is inserted, and in the same genus between the scuta, terga, and carina and the summit of the stalk small accessory pieces occur; and if one imagines a disappearance of the stalk of such a form, an enlargement of these accessory pieces, usually six in number, and their articulation to form a wall-like circle around the body of the animal, the scuta and terga closing it in and forming as it were a roof, an idea of the arrangement of the shell of *Balanus*, the acorn-barnacle, will be obtained.

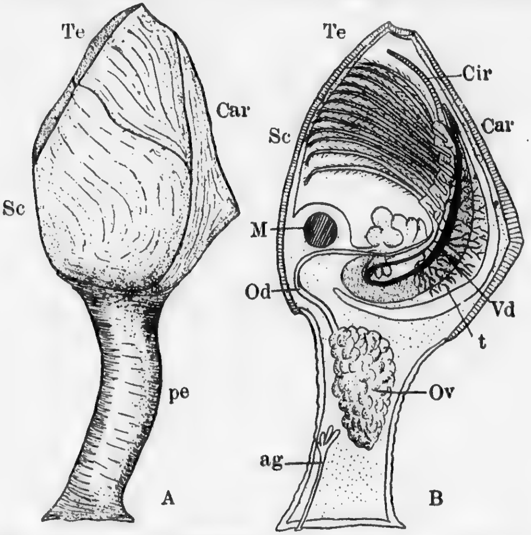

FIG. 181.—*Lepas fascicularis.* *A*, exterior; *B*, structure.

ag = antennary gland.
Car = carina.
Cir = cirrus
M = shell-muscle.
Od = oviduct.
Ov = ovary.
pe = peduncle.
Sc = scutum.
t = testis.
Te = tergum.
Vd = vas deferens.

No special respiratory organs exist, the entire surface of the body probably performing this function, nor does a heart seem to occur in any member of the group. The nervous system consists in *Lepas* of a syncerebrum and five or six ventral ganglia,—of which the last is probably composed of at least two fused ganglia, and a certain amount of fusion has also probably occurred in the first. In *Balanus* the fusion has reached its greatest extent, the entire ventral chain of ganglia having fused to a single mass. The median unpaired eye is usually represented, and in some forms rudimentary lateral eyes are present, showing, however, a marked degeneration from the large compound eyes which occur in the Cypris-like larva.

As a rule the Cirrhipedia are hermaphrodite in accordance with their sessile or parasitic life. The testes (Fig. 181, *B*, *t*) lie one on each side of the digestive tract, and the vasa deferentia (*vd*) after dilating into seminal vesicles pass to the long cirrus (*cir*) borne by the abdomen, at the tip of which they open by a short common duct. The ovaries lie in *Lepas* (Fig. 181, *B*, *ov*) in the stalk, and in stalkless forms, such as *Balanus*, in the basal fold which corresponds to the stalk, and the oviducts (*od*) passing upwards and then backwards open on the basal joints of the anterior thoracic appendages. Although hermaphroditism is the rule throughout the order, yet in some cases small males have been found which have received the name of "complemental" males. These occur in the genus *Ibla* and in some species of *Scalpellum* and live like parasites in folds of the mantle of the hermaphrodite forms. In form they do not advance greatly beyond the Cypris stage, and possess in addition to the antennules only four pair of small thoracic limbs, the mandibles and maxillæ as well as the mouth being entirely wanting, while the digestive tract is rudimentary. In other species of *Scalpellum*, and in the genera *Alcippe* and *Cryptophialus*, these pigmy males are also present, but the forms in which they live are no longer hermaphrodites but females, so that bisexuality with sexual dimorphism occurs in these forms.

It might be supposed from the general occurrence of bisexuality among the Crustacea that these last cases represented the first stage in the disappearance of the males, leading finally to hermaphroditism. Since, however, *Alcippe* and *Cryptophialus* are the most degenerate of the Cirrhipeds so far discussed, it would seem that this is not the case, but rather that, on the assumption of a sessile life hermaphroditism became characteristic of the order, the bisexualism of these boring forms being secondarily acquired. The fact that the pigmy males present larval characters suggests the idea that their occurrence may be an extreme case of proterandry. If in the hermaphrodite forms it is a rule that the spermatozoa mature earlier than the ova, thus preventing self-fertilization, it is conceivable that this early maturation of the testes might be carried back almost to the Cypris stage and pigmy males be thus developed.

Not unfrequently barnacles choose the bodies of other animals upon which to fasten, as for instance upon the carapace of *Limulus*, or on the skin of whales, and the genus *Anelasma* fastens itself upon the surface of the body of a Shark, its stalk penetrating into the tissues and developing rootlike processes and so enabling it to lead a parasitic life. As a result of this the calcareous plates cease to develop, the mantle having merely a leathery consistency and the mandibles and maxillæ remain rudimentary. This degeneration is carried still further in *Proteolepas* (Fig. 182), which lives as a parasite in the mantle-cavity of other Cirrhipeds and has a maggotlike appearance, the body being distinctly divided into eleven segments and lacking all traces of a mantle. The mouth-parts are modified so as to be suctorial, and the thoracic feet are entirely wanting, while the digestive tract becomes rudimentary. Finally, a group of forms, known as the *Rhizocephala*, fasten themselves to the abdomen of crabs and become transformed into cylindrical or saclike structures entirely destitute of digestive tract and appendages, rootlike processes arising from the anterior end of the body and traversing the body of the host, by whose juices the parasite is nourished. The genus *Sacculina* consists of an anterior short cylindrical portion from the extremity of which the rootlike processes arise and which perforates the integument of the host. From the base of this a circular fold arises

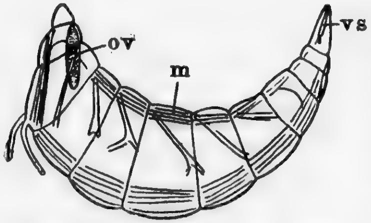

FIG. 182.—*Proteolepas* (from BRONN).
m = muscle.
ov = ovary.
vs = vesicula seminalis.

which encloses between its walls and the wall of the body a cavity which serves as a brood-pouch and communicates with the exterior by a terminal opening capable of being closed by a sphincter. The body proper contains only the nervous system, reduced to a single ganglion, and the ovaries and the paired testes, as well as a pair of cement-glands connected with the female genital openings.

The development of *Sacculina* presents some extraordinary features. It resembles in its early stages the development of the other Cirrhipeds and reaches a typical Cypris stage during which it fastens itself by the antennules to the body of a crab. The tissues of the larva then retract themselves from the cuticle, and a remarkable degeneration of the body together with an amputation of the entire thoracic and abdominal regions then ensues, leaving an oval mass of tissue, richly pigmented, attached to the body of the crab by the empty cuticle of the antennules. At the anterior end of this mass a hollow dartlike process arises which is pushed forward through the hollow cuticle of the antennules and pierces the body-wall of the host, the parasite apparently flowing then through the dart and so becoming an endoparasite. Within the body of the crab the development of the *Sacculina* takes place from the apparently undifferentiated mass of tissue by which it is represented, and growing rapidly produces an absorption of the ventral integument of the host, which allows the saclike body to protrude to the exterior. It is to be noted that parasitic Cirrhipeds (*Laura*) have been found in the stem of a Gorgonian and also in the body-cavity of Echinoderms (*Dendrogaster*). These forms show many peculiarities of structure and have been grouped together in the suborder Ascothoracida.

II. CLASS **Malacostraca.**

The Malacostraca are distinguished from the Entomostraca by the definiteness throughout the entire class of the number of metameres entering into the composition of the body. The head consists of five segments which are invariably fused, and the thorax is composed of eight, of which the anterior one, or indeed all, may unite with the head to form a perfect or imperfect cephalothorax. The abdomen is the only region in which variation of number takes place, and this variation is confined to a single group of forms (Leptostraca). In these the abdomen is composed of eight segments, while in all other forms it possesses only seven, counting in both these cases the terminal segment which bears the anus and is known as the telson. All these segments with the exception of the telson, and in the Leptostraca of the segment immediately in front of it, bear appendages. Folds of the integument forming a cephalothoracic carapace are frequently present, but it is rare that a bivalved shell occurs.

The stomach is always provided with chitinous teeth and forms an efficient masticatory organ, and lateral eyes are present except in some Cumacea and in some forms belonging to other groups which inhabit caves or the depths of the ocean, under which conditions the eyes become rudimentary. The openings of the female reproductive organs are always situated on the basal joints of the appendages of the sixth thoracic segment, and the male openings on the appendages of the eighth segment. The antennary gland is usually well developed, while the shell-gland is either rudimentary or wanting in the adult.

Although numerous rather small forms belong to this class, yet on the whole they much surpass in size the Entomostraca, some forms even reaching a length of over 50 cm. A few forms, such as *Euphausia* and *Penœus*, leave the egg as a Nauplius, but in the majority this stage is passed before hatching, the embryo first leading a free existence at a later stage in the larval form known as the *Zöea*, though in some cases hatching may be retarded until later stages, in fact sometimes until the adult form is acquired.

I. Subclass **Leptostraca.**

The Leptostraca are exceedingly interesting forms, presenting similarities to the Entomostraca on the one hand and to the Malacostraca on the other, thus connecting the two classes. They are exclusively marine in habitat and possess a thin bivalved shell-duplicature which is provided with an adductor muscle and is prolonged in front into an unpaired plate which covers the dorsal surface of the head.

The antennules (Fig. 183, *at*^{1}) consist of a three-jointed basal portion bearing in addition to the multiarticulate flagellum a scalelike exopodite, a structure wanting in the antennæ (*at*^{2}), which otherwise have a similar form. The mandibles bear a palp, as do also the first maxillæ, it being in these latter appendages prolonged into a long slender limblike (*mx*) structure which is directed dorsally and serves for cleansing the inner surface of the shell. The second maxillæ are biramous foliate structures, as are also the eight thoracic appendages (*t*), each of which bears upon its basal joints a platelike epipodite which is respiratory in function. The four anterior abdominal appendages (ab^4) are strong biramous swimming-legs, while the two posterior are small and uniramous. Behind the last appendage-bearing segment are two others without appendages, the terminal one being the telson, the Leptostraca possessing one more metamere than the rest of the Malacostraca.

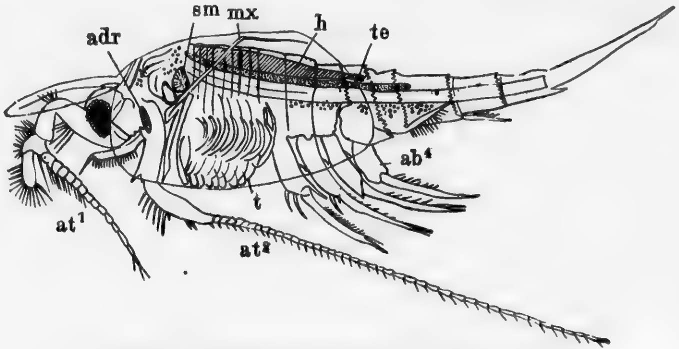

FIG. 183.—*Nebalia Geoffroyi*, MALE (after CLAUS).

ab^4 = abdominal appendage.
adr = antennary gland
at^1 = antennule.
at^2 = antenna.
h = heart.
mx = process of first maxilla.
sm = shell-muscle.
t = thoracic appendage.
te = testis.

The heart is an elongated organ extending from the maxillary region as far back as the fourth abdominal segment; it possesses several ostia, and is prolonged anteriorly and posteriorly into aortæ. The antennary gland is present and a rudimentary shell-gland also persists. The lateral eyes are borne upon short stalks.

The group contains but few species, the majority belonging to the genus *Nebalia* (Fig. 183).

II. SUBCLASS **THORACOSTRACA.**

The Thoracostraca are characterized by the occurrence throughout the group of a well-developed duplicature of the body-wall, arising from the posterior head-segments and covering in a greater or less number of the thoracic segments, constituting what is termed a carapace. On the dorsal surface it fuses with the body-wall, but, at the sides encloses a respiratory chamber in which the branchiæ, when present, lie. According as the carapace extends over all or only over the anterior thoracic segments a more or less perfect cephalothorax is formed, a fusion of the covered thoracic segments with each other and with the head-segments occurring, the abdominal segments remaining in all cases distinct.

Branchiæ, consisting of bunches of hollow thin-walled processes whose cavities communicate with the lacunar spaces of the body, are borne by certain of the appendages except in the Mysideæ. The lateral eyes except in the Cumacea are stalked and the antennary gland is usually well developed.

1. Order **Schizopoda.**

The carapace in the Schizopoda covers in the entire thorax, but a certain number of the posterior thoracic segments remain ununited with it. The antennules are biramous, as are also the antennæ (Fig. 184), the exopodite in the latter case being represented by a scalelike structure. The thoracic appendages are all similar and are biramous, the endopodites being limblike structures tipped by claws, while the exopodites are multiarticulate flagella. In the genus *Euphausia* the two last pairs are quite rudimentary, their branchiæ remaining, however, well developed. The two anterior pairs in the genus *Mysis* have their basal joints enlarged to form jaws and consequently are distinguished as maxillipeds, but in *Euphausia* this distinction does not occur. The abdominal appendages in the females are generally small with the exception of the sixth pair, and in the genus *Mysis* are quite rudimentary. In the males of all genera they are, however, well-developed biramous swimming-feet, and the sixth pair in both sexes forms with the telson a tail-fin.

Branchiæ are present in *Mysis* only in the form of small epipodial elevations of the thoracic appendages, and in *Siriella* as coiled tubular structures on the protopodites of the abdominal appendages of the males. In *Euphausia*, however, they form large ramified bunches attached to the protopodites of the thoracic limbs and are present even on the rudiments of the seventh and eighth pairs; they are not, however, enclosed within a chamber formed by the lateral portions of the carapace, but project freely to the exterior.

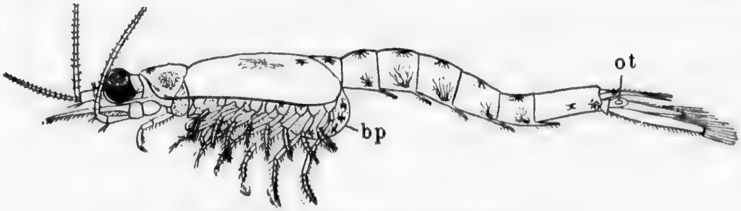

FIG. 184.—*Mysis relicta* (after SARS).
bp = brood-pouch. *ot* = otocyst.

Otocysts occur in the inner lamellæ of the sixth abdominal appendages (Fig. 184, *ot*), and in *Euphausia* a number of eye-like phosphorescent organs occur on the basal joints of the second and seventh thoracic appendages as well as upon the ventral surface of the four anterior abdominal segments. They are spherical in shape and each consists of a cup of cells containing red pigment covered in by a lens.

The Schizopoda are essentially marine, though some species of the genus *Mysis* (Fig. 184) occur in fresh and brackish water.

2. Order **Cumacea.**

In this order the carapace covers only the anterior three or four thoracic segments, five or four of them remaining distinct. The antennules are short and in the male biramous, while the antennæ, though in the female almost rudimentary, may be as long as the entire body. The two anterior thoracic appendages form maxillipeds, their basal joints serving for mastication while the succeeding six pairs are limblike, all but the last or three last possessing small exopodites. The

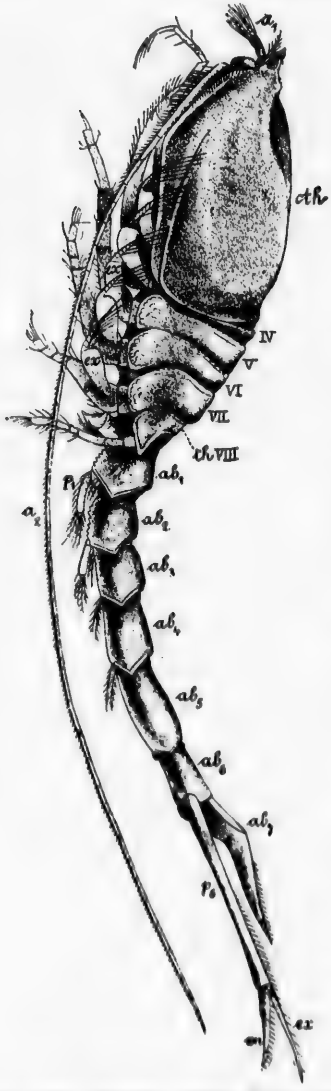

FIG. 185.—*Diastylis stygia*, MALE (after SARS from LANG).

a_1 = antennule.
a_2 = antenna.
ab = abdominal appendages.
cth = carapace.
en = endopodite.
ex = exopodite.
p = abdominal appendages.
IV–VIII = thoracic segments.

sixth abdominal segment bears a pair of biramous appendages with a long single-jointed protopodite, the remaining segments being in the female destitute of appendages, but in the male the anterior 2 (*Diastylis*), 3, or 5 (*Campylaspis*) segments may bear biramous swimming-feet.

The lateral eyes are never stalked and may be closely approximated or even fused on the dorsal surface of the cephalothorax. They are generally composed of but few ommatidia and in some species are entirely wanting.

The Cumacea are exclusively marine and are more especially characteristic of the colder seas.

3. Order **Stomatopoda.**

As in the Cumacea the carapace covers only some of the anterior thoracic segments, the last three or four remaining distinct, but the abdomen, instead of being slender, is even stouter than the thorax and ends in a terminal tail-fin. The anterior portion of the head, bearing the eyes and the two pairs of antennæ, is separated from and movable upon the rest of the cephalo-thorax, and only the more anterior thoracic segments are fused with the carapace, though it covers in several others.

The antennules consist of an elongated three-jointed basal portion bearing three many-jointed flagella, while the antennæ are generally shorter, the exopodite being represented by a large scale. The maxillæ are comparatively small, and the appendages of the five anterior thoracic appendages are crowded forwards and are termed maxillipeds, being limb-like structures destitute of exopodites, but possessing well-developed epipodites, and with the terminal joint capable of flexion upon the next succeeding one. The second maxilliped is especially long and large, and with its strong terminal and penultimate joints forms a very efficient weapon for securing prey. The three posterior appendages of the thorax are slender biramous structures, the somewhat stronger abdominal appendages being also biramous and somewhat lamellar swimming-feet. The last pair are especially enlarged and directed backwards, forming with the telson the strong tail-fin.

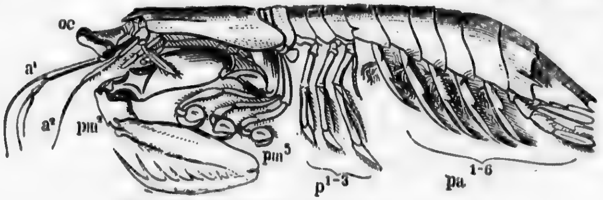

FIG. 186.—*Squilla mantis* (from LEUNIS).

a^1 = antennules.
a^2 = antennæ.
oc = compound eyes.
pm = maxillipeds.
p = thoracic limbs.
pa = abdominal limbs.

Bunches of branchial filaments occur upon the outer lamellæ of the abdominal appendages with the exception of the last pair. The heart is much elongated, extending from the anterior thoracic region as far back as the fifth abdominal segment and possessing numerous pairs of ostia. It is prolonged anteriorly and posteriorly into aortæ and gives off laterally in each segment a pair of arteries.

The Stomatopods are all marine and pass through a complicated series of metamorphoses during development. Some of the principal genera are *Squilla* (Fig. 186), *Lysiosquilla*, and *Gonodactylus*.

4. Order **Decapoda.**

In the Decapods the carapace is well developed, covering in the thorax completely (Fig. 162), the segments of that region of the body fusing with it dorsally, so that a perfect cephalothorax is present. The antennules generally possess two terminal multiarticulate flagella, and the antennæ frequently lack the scalelike exopodite which occurs in other groups (e.g., Schizopoda). In the second maxillæ the exopodite is transformed into a platelike structure which, swinging to and fro, serves to renew the water in the branchial chamber lying between the lateral portions of the carapace and the body-walls. On account of this action this appendage is usually spoken of as the *scaphognathite.* The three anterior thoracic appendages are maxillipeds, the third one frequently becoming almost limblike, a characteristic which distinguishes the five posterior pairs of appendages which are adapted for walking and are hence termed the *pereiopods.* They lack all traces of exopodites, though usually bearing epipodites and branchiæ, and a certain number of the anterior ones are frequently chelate, thus serving for the prehension of food. The number of the pereiopods has suggested the name given to the order. The abdominal appendages are sometimes wanting or very rudimentary, but when present are biramous swimming-feet and are hence termed *pleopods*—a term equally applicable in some other groups.

The branchiæ lie entirely within the branchial chamber and are developed in connection with the thoracic appendages. They may be seated upon the basal joints of the appendages (podobranchia), or upon the joint between the appendage and the body-wall (arthrobranchia), or finally upon the body-wall itself (pleurobranchia). All three kinds may occur on the same segment, so that the entire number of gills may be much greater than that of the appendages, amounting in the Lobster to no less than twenty in each branchial chamber.

The heart is a short saclike organ lying in the thorax and possessing as a rule three pairs of ostia, one pair being situated on the dorsal surface, one upon the sides, and the third on the ventral surface. Arteries pass off from both ends of the heart. Otocysts are always developed in the basal joints of the antennules.

1. Suborder *Macrura*.

In the Macrura the abdomen is well developed and usually as long as the cephalothorax, and is provided with its full complement of appendages, the sixth pair forming with the telson a tail-fin. Exceptions to these arrangements occur; in the Hermit-crabs, *Eupagurus*, which inhabit the empty shells of Gasteropod Mollusks, the abdomen is generally soft and unsymmetrical, since it is coiled around the columella of the shell, but terminates in a movable tail-fin which serves, together with the remaining pleopods and the last (and sometimes also the penultimate) pereiopod, which is bent dorsally, to retain the animal in the shell. The chelæ of the anterior pereiopods are generally unequal in size, serving to occlude the mouth of the shell, and occasionally the abdominal appendages of only one side are developed. In the genus *Hippa* too the abdomen, though with a well-developed and calcified cuticle, is short, the terminal half being bent up under the thorax, the condition characteristic of the Crabs being thus approached. In some forms, such as *Sergestes* and *Lucifer*, the fourth and fifth pereiopods may be rudimentary or even absent, but more usually all these appendages are well devel-

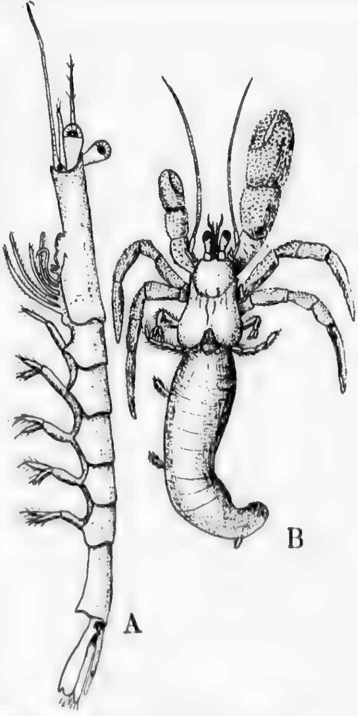

FIG. 187.—*A*, A YOUNG *Lucifer* (adapted from BROOKS); *B*, *Eupagurus bernhardus* (after LEUNIS).

oped, the anterior ones becoming chelate. In the Crayfish, *Cambarus*, and the Lobster, *Homarus*, the first pereiopod is an exceedingly strong chela, and the same arrangement is found in *Alpheus*, while in the Shrimp, *Palæmonetes*, the second pereiopod is somewhat longer than the first.

The branchiæ are usually numerous and are for the most part bunches of cylindrical processes, but in *Palæmonetes* and the shrimps and prawns in general, which form the family Carididæ, [illegible] in the Hermit-crabs they are lamellate. In *Lucifer* branchiæ are entirely wanting. The Macrura are essentially marine, a few forms, such as *Cambarus* and some species of *Palæmon*, occurring in fresh water. The genus *Birgus*, one of the Hermit-crabs, commonly known as the robber-crab, is almost entirely terrestrial, living in holes in the ground and climbing cocoa-nut palms for the sake of the nuts, on which it lives. In harmony with its terrestrial life the inner surface of the branchial chamber is thrown into folds richly supplied with blood-lacunæ, a lunglike structure, recalling the lungs of the Pulmonate Gasteropods, being thus developed.

2. Suborder *Brachyura*.

In the Brachyura the body is exceedingly compact, the abdomen being very much reduced in size and usually destitute of a tail-fin, and in addition is bent up so as to lie in a groove upon the ventral surface of the cephalothorax. In some cases the cephalothorax is almost globular, though prolonged anteriorly into a strong rostral spine, as in *Libinia*, the spider-crab; while in other cases it is more flattened and triangular in shape and lacks a distinct rostrum, as in the edible crab, *Callinectes*, the lady-crab, *Platyonychus*, and the common crab, *Cancer*, and in others again is more or less quadrangular and thicker, as in *Pinnotheres*, the oyster-crab, *Ocypoda*, the sand-crab, and *Gelasimus*, the fiddler-crab. Th

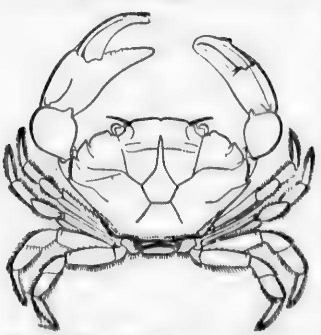
FIG. 188. — *Panopæus depressus* (after EMERTON from VERRAL).

antennules are small and they and the eyes can be partially concealed in a groove on the anterior edge of the carapace. The abdominal appendages, with the exception of the anterior one or two pairs which are adapted for copulation, are absent in the males, while the females generally possess four pairs, to which the ova are attached.

The gills are generally few in number, except in *Porcellana* and some allied forms, and are usually lamellate in form. While essentially marine in habit, the Brachyura are frequently more or less terrestrial, the sand-crabs, *Ocypoda*, and the fiddler-crabs, *Gelasimus*, living in holes in the sand just above high-tide mark, while the land-crabs, *Gecarcinus*, of the tropics may live some distance from the sea, migrating to it in armies during the breeding-season. A few forms, such as the genus *Telphusa*, are aquatic.

III. Subclass **ARTHROSTRACA.**

The Arthrostraca, with the exception of the small group of the Anisopoda, are destitute of a carapace, and the thoracic appendages, with the exception of the first pair, are jointed walking-limbs lacking an exopodite. The anterior, or in some cases the anterior two thoracic segments fuse with the head, the appendages of these segments differing from those of the free segments, being modified to assist in the process of mastication, whence they are termed maxillipeds. The abdomen is composed of six segments provided with appendages, and of a terminal telson; occasionally the various segments fuse together, and in some forms the abdomen is reduced to a small unsegmented structure. Platelike appendages attached to the basal joints of some of the thoracic limbs form by their meeting and overlapping a brood-pouch in which the ova undergo their development.

The lateral compound eyes are not, except in *Tanais*, supported on stalks, a characteristic which has suggested the term *Edriophthalmata* sometimes applied to the group.

1. Order **Anisopoda.**

The Anisopoda are exclusively marine forms in which the two anterior thoracic segments are fused with the head and covered in at the sides by duplicatures of the body-wall, which enclose a small respiratory cavity.

The antennules and antennæ are uniramous except in *Apseudes* in which the antennules carry two terminal flagella. The palps of the anterior maxillæ project into the respiratory chamber and serve for cleansing it, and the first thoracic limbs, the maxillipeds, bear each an epipodial branchial appendage lying in the respiratory chamber. This limb and the succeeding one are chelate, the inner angle of the penultimate joint being prolonged into a process against which the terminal joint may be apposed. The abdominal appendages are biramous swimming-feet in *Tanais* and *Apseudes*, the last pair being in *Anthura* especially enlarged to form with the telson a terminal finlike structure.

2. Order **Isopoda.**

The majority of the Isopoda are marine, the genus *Asellus* (Fig. 189), however, occurring in fresh water, while *Oniscus*, *Porcellio*, and *Armadillidium* are terrestrial, being commonly known as Wood-lice or Sow-bugs. The body in all forms is more or less flattened dorso-ventrally and only the anterior thoracic segment is fused with the head, the remaining seven remaining perfectly distinct. There is no trace in the adult of a carapace, and the abdominal segments are usually small and may be fused more or less completely.

The maxillæ are destitute of palps and the maxillipeds (*mxp*) usually fuse together to form a sort of lower lip. The remaining thoracic appendages are limblike and do not bear any respiratory appendages, though lamellæ are attached to the basal joints of several of them in female individuals, serving to form a brood-pouch. The five posterior abdominal appendages are biramous and lamellar (*ab*), serving both for swimming and for respiration, the anterior pair (*op*) usually becoming hard and forming an operculum which covers in the posterior more delicate appendages and in the terrestrial forms may have branching spaces containing air (tracheæ) ramifying through them.

The heart (*ht*), in conformity to the position of the respiratory organs, is situated principally in the abdomen, extending forwards only a short distance into the thorax segment. It possesses one or two pairs of ostia and is closed behind, giving off in front and at the sides numerous aortæ. A shell-gland has been observed in some Isopoda, but the antennary gland is wanting.

Although the majority of the marine forms, such as *Idotea* and *Sphæroma*, lead a free existence, nevertheless there are certain parasitic forms. Thus the genera *Cymothoa* and *Æga* are parasitic on the skin or in the mouth of fishes, but also retain the power of swimming and consequently are not much modified. The genus *Bopyrus*, which lives in the branchial cavity of shrimps, becomes in the female somewhat distorted in shape and asymmetrical, and the mouth-parts become transformed into a suctorial proboscis and the eyes disappear. The male, however, which is much smaller than the female, retains the eyes and does not depart from the usual symmetrical body form. The degeneration of the female proceeds much farther in the genus *Entoniscus*, which lives either partly or wholly included within the body-cavity of other Crustacea and assumes a saclike unsymmetrical form, recalling to a certain extent that of some of the parasitic Copepoda. At the time of pairing both sexes are alike fully segmented and with an almost full complement of appendages.

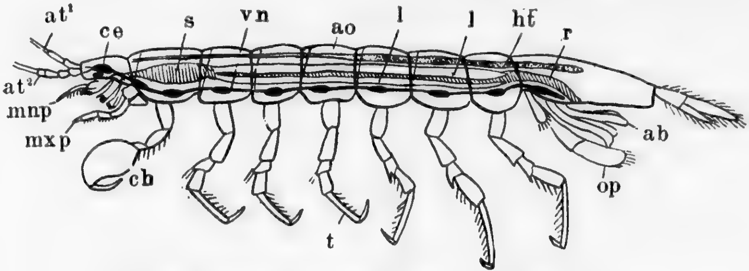

FIG. 189.—*Asellus communis*, DIAGRAM OF STRUCTURE.

ab = abdominal appendages.
ao = aorta.
*at*¹ = antennule.
*at*² = antenna.
ce = cerebral ganglion.
ch = chelate limb.
ht = heart.
l = liver-cæca.
mnp = mandibular palp.
mxp = maxilliped.
r = rectum.
s = stomach.
t = thoracic appendage.
vn = ventral nerve-cord.

After copulation, however, the female assumes the degenerated form, while the male dies.

3. Order **Amphipoda.**

Like the Isopoda these are essentially marine forms, though the genus *Gammarus* is aquatic and *Orchestia* (Fig. 190) partly terrestrial, living among the wrack on sea-beaches just beyond the reach of the waves. The body in the Amphipoda is laterally flattened and presents therefore a very different appearance from that of the Isopoda, though, as in that group, lacking all traces of a carapace. The first thoracic segment is fused with the head, and in *Caprella* and *Cyamus* the second segment likewise. The appendages of the head and the maxillipeds resemble those of the Isopoda, and the remaining thoracic appendages are limblike, a certain number of the anterior ones frequently possessing a terminal joint capable of flexion upon the succeeding one, or even being chelate. The five posterior limbs or the third and fourth only bear epipodial lobes which serve as branchiæ, and

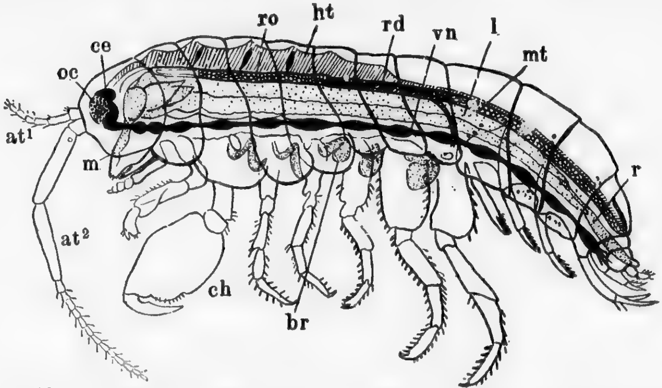

FIG. 190.—DIAGRAM OF STRUCTURE OF *Orchestia cavimana* (after NEBESKI).

*at*¹ = antennule.
*at*² = antenna.
br = branchia.
ce = cerebral ganglion.
ch = chelate limb.
ht = heart.
l = liver-cæca.
m = mouth.
mt = Malpighian tubule.
oc = eye.
r = rectum.
rd = reproductive duct.
ro = reproductive organ.
vn = ventral nerve-cord.

a number of the limbs also in females bear lamellæ which may enclose a brood-pouch. The three anterior abdominal limbs are biramous and serve for swimming, while the three posterior ones, also biramous, are frequently directed backwards and serve as springing organs, the springing powers of *Orchestia* having gained for it the name of the Beach-flea. In *Caprella*, which crawls about over colonies of Hydroids and Polyzoa, and *Cyamus*, which is parasitic upon the skin of whales, the abdomen becomes almost rudimentary and is destitute of appendages.

The heart (*ht*) lies in the thoracic region in the anterior five or six segments and possesses from one (*Corophium*) to three ostia. It is prolonged into an aorta at either end. In connection with the mid-gut portion of the digestive tract, in addition to the four so-called liver-cæca (*l*) is a pair of glandular cæca which seem to be excretory in function and have been termed Malpighian tubules (*mt*). An antennary gland occurs, but the shell-gland is apparently unrepresented in adults.

Development of the Crustacea.—The majority of the Crustacea pass through a more or less complicated series of metamorphoses, the larval forms being highly suggestive when studied from the phylogenetic standpoint. A few forms, especially those inhabiting fresh water, abbreviate their development considerably, so that the young animal when it leaves the egg practically may differ from the parent only in size (*Cambarus*), and among the higher forms the development is generally abbreviated to the extent that a greater or less number of the larval stages, characteristic of lower forms, are passed through while the young animal is still within the egg-membrane, only the final stages being free-swimming.

Throughout the Entomostraca the first larval form which hatches from the egg is termed the *Nauplius* (Fig. 191) and differs markedly from the adult, chiefly, however, in the small number of appendages it possesses. The body in typical forms shows no trace of segmentation and possesses a single median eye generally x-shaped. But three pairs of limbs are present, which become transformed later into the antennules, antennæ, and the mandibles of the adult. The Naupliar antennules are uniramous and, like the other limbs, but indistinctly jointed, the antennæ and mandibles being, however, biramous and possessing strong setæ at their bases which function as jaws, though both pairs of appendages are essentially locomotor. Judging from the appendages, therefore, the Nauplius may be regarded as consisting of five segments, one corresponding to the prostomial lobe of Annelids and containing the primitive cerebral ganglion (archicerebrum), one corresponding to each pair of appendages and one to the region of the body behind the mandibles.

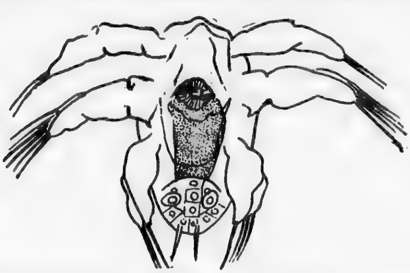

FIG. 191.—NAUPLIUS OF *Cetochilus septentrionalis* (after GROBBEN).

A Nauplius of this simple form may be regarded as typical and is that which is found in the majority of the Copepoda and in the Cirrhipedia as well as in some Branchiopoda (*Estheria*, *Limnadia*). In the Ostracoda the arrangement of the limbs and segments is the same, but the bivalved shell characteristic of the adult is already developed, giving the Nauplius an appearance very different from that of the Copepoda. Not unfrequently, however, as for instance in *Apus* among the Branchiopoda, and *Leptodora* among the Cladocera (the remaining Cladocera, so far as is known, leave the egg with the adult form), the Nauplius, though possessing only the three pairs of appendages, yet shows indications in the post-mandibular region of a varying number of additional segments, and to this form it is convenient to apply the name *Metanauplius*.

As a rule in the Entomostraca further development consists of a series of moults (ecdyses), an increase in the number of segments and appendages and modifications of the latter taking place at each ecdysis, until the adult form is attained. No special larval forms beyond the Nauplius are common to all the members of the class, and it is only in the Cirrhipedia that a second definite larval form can be distinguished, the Cypris-larva, to which attention has already been called (p. 399).

In the Malacostraca the occurrence of a free-swimming Nauplius is the exception rather than the rule, and indeed larval forms are practically wanting in some groups, such as the Leptostraca and Arthrostraca, and in certain species or families of other groups (e.g. *Mysidæ*, *Cambarus*). In the genus *Penæus* among the Decapods, and in *Euphausia* among the Schizopods, a typical free-swimming Nauplius occurs, and in *Lucifer* the embryo leaves the egg in the form of the Metanauplius. In the majority of forms these stages are passed over while the embryo is still within the egg-shell, and it hatches only when it has acquired a greater degree of development. In such forms as *Penæus*, *Euphausia*, and *Lucifer* the Metanauplius stages pass into what is termed the *Protozoëa* (Fig. 192, *A*) a stage also passed over within the egg by the majority of Malacostracans, though occurring as the first larval stage of some Stomatopods. It is characterized by the development of two maxillæ and the two or three anterior

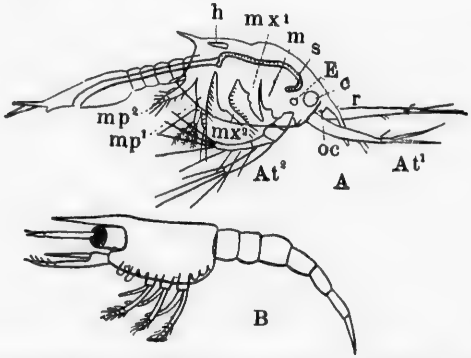

FIG. 192.—*A*, PROTOZOËA OF *Lucifer* (after BROOKS); *B*, ZOËA OF *Palæmonetes* (after FAXON).

*At*¹ = antennule.
*At*² = antenna.
c = cerebral ganglion.
E = compound eye.
h = heart.
m = mandible.
*mx*¹, *mx*² = maxillæ.
*mp*¹, *mp*² = maxillipeds.
oc = simple eye.
r = rostrum.
s = stomach.

thoracic appendages in addition to those already present in the Nauplius, and furthermore by the distinct separation of the body into an anterior cephalo-thoracic portion covered by a carapace and a posterior abdomen which is usually but imperfectly segmented. This stage is succeeded sometimes after two or more ecdyses by the *Zoëa* (Fig. 192, *B*), a stage in which the majority of Decapoda leave the egg. It is distinguished from the Protozoëa principally by the perfect segmentation of the abdominal region, though it still possesses no appendages, unless it be rudiments of the sixth pair, and it is furthermore characterized by the compound eyes being stalked, a feature but slightly indicated in the Protozoëa, in which stage they make their appearance. The Zoëa stage in the Brachyura is generally characterized by the development of spines, sometimes of enormous length (*Porcellana*), upon the dorsum and sides of the carapace.

In such a form as *Euphausia* the next stage is the adult, but in the Decapods other larval stages intervene before the adult condition is reached. The first of these is characterized in the majority of the Macrura by the appearance of the remaining thoracic appendages which were unrepresented in the Zoëa, in the form of biramous structures closely resembling the thoracic appendages of the Schizopoda, whence the stage is generally termed the *Mysis* stage (Fig. 193). The abdominal appendages also develop during this stage. Among the Hermit-crabs (Paguridæ) and the Brachyura the development is to a certain extent abbreviated, the pereiopods never being represented by biramous appendages, but being from the first uniramous, and in these forms therefore a true Mysis stage never occurs. To the corresponding stage,

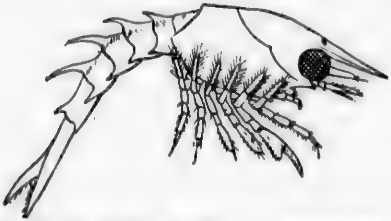

Fig. 193.—Mysis stage of Lobster, *Homarus americanus* (after S. I. Smith).

or rather to one in which the pereiopods are indicated but not fully developed, the term *Metazoëa* is applied. Furthermore in certain Macrura, such as *Scyllarus* and *Palinurus*, the Mysis stage is represented by peculiarly-shaped transparent larvæ which have been termed *Phyllosoma*, or glass-crabs. The carapace is divided into two portions, of which the anterior or larger covers in the head region and the posterior the thorax, the body being throughout flat and the abdomen very small. The pereiopods, of which in the earliest stages there are but three, are biramous, and the first maxillipeds are either entirely wanting or very rudimentary. During successive ecdyses the missing appendages are gradually developed, though the actual transformation of the *Phyllosoma* into the youngest *Scyllarus* or *Palinurus* stage (which is decidedly smaller than the oldest *Phyllosoma*) has not yet been observed.

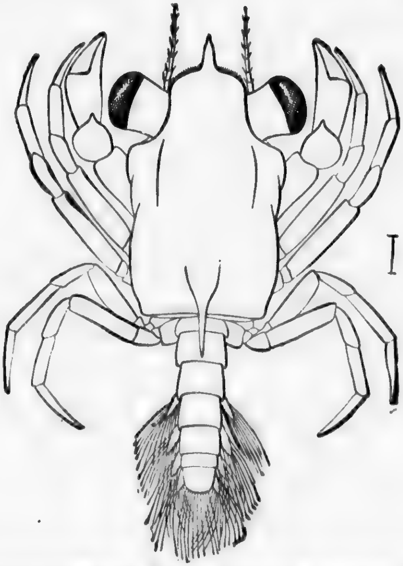

FIG. 194.—MEGALOPA-STAGE OF *Cancer irroratus* (after EMERTON from VERRILL).

The change from the Mysis stage to the adult is usually gradual, and no specially definite larval forms are to be found as a rule among the Macrura. In the Brachyura, however, the Metazoëa becomes transformed into a well-marked form, the *Megalopa* (Fig. 194), so called from the usually large size of the cephalothorax. It resembles closely a Macruran, differing only in the abdomen being relatively small, and becomes converted into the adult form by the doubling of the abdomen beneath the thorax. A Megalopa stage occurs also in the Hermit-crabs, but is not so well marked off from the young fully-formed animals as in the Brachyura.

Affinities of the Crustacea.—The relationships of the higher groups of the Malacostraca to one another are clearly shown by their larval forms, the Megalopa showing the origin of the Brachyura from Macruran forms, and the Mysis stage that of the latter from Schizopod ancestors. When attempts are made to go still further difficulties stand in the way. As regards the Stomatopoda it is to be noted that they pass through a stage, the *Erichthus*, in which the thoracic appendages which are present are biramous, and it seems probable that both they and the Cumacea are referable back to Schizopod ancestors. The Arthrostraca, on the other hand, are probably traceable to Cumacealike ancestors, while the Leptostraca represent more nearly the Entomostracan ancestors than any other group, though widely differentiated from them in certain particulars. It is even still more difficult to trace out relationships of the various Entomostracan orders, but it seems fairly clear that Phyllopodan forms such as *Apus* are to be considered as representing more nearly than any others the primitive Crustacea.

As regards the affinities with other groups very interesting questions arise, two possibilities seeming to be open. According to one the Crustacea have been derived directly from segmented Annelids, through forms represented in a modified condition to-day by *Apus*. The lobed appendage of *Apus* is a modified parapodium, and the segmentation of the body has been inherited. What then as to the Nauplius? According to this view it has practically no ancestral significance, or at best can be considered only as representing a Trochophore larva highly modified and with many adult characters thrown back upon it. This latter idea does not seem, however, to agree with the facts, since the Trochophore is an unsegmented structure and can be comparable only to the prostomial and first appendage-bearing segments of the Nauplius. In other words, the Nauplius is comparable, if comparable at all, to a Trochophore *plus* certain additional segments. It has recently been suggested that possibly the Nauplius may represent not the Trochophore but the larval Annelid with three parapodia, which, as indicated (p. 215), is a well-marked stage in the development of many Polychæta. The number of segments is apparently similar in the two forms, and the idea is plausible. If, however, in all Crustacea a ganglion, representing a segment, intervenes between the archicerebral ganglia and the antennulary (see p. 378), then the Nauplius has potentially one segment more than the Annelid larva and the comparison will not hold. If the direct Annelid origin is to be accepted, it seems most satisfactory at present to regard the Nauplius as a secondarily acquired larval stage without any ancestral significance.

Another suggestion has, however, been made which gives the Nauplius a significance and traces the Crustacea back to unsegmented ancestors. It is to the effect that the Nauplius can be referred to Rotiferlike ancestors, the remarkable *Hexarthra* with its six processes being supposed to indicate the line of descent. It is exceedingly doubtful, however, whether this similarity can be regarded as anything more than a superficial one

TYPE CRUSTACEA.

I. Class ENTOMOSTRACA.—Number of segments varies; abdomen without appendages; larva a Nauplius.

1. Order *Phyllopoda.*—Number of segments variable; appendages with branchiæ.

1. Suborder *Branchiopoda.*—Body plainly segmented and segments of thorax more numerous than six. *Apus, Branchipus, Estheria, Limnadia, Limnetis.*

2. Suborder *Cladocera.*—Body indistinctly segmented; with bivalved shell; four to six thoracic appendages. *Daphnia, Moina, Sida, Evadne, Polyphemus.*

2. Order *Ostracoda.*—With bivalved shell; body indistinctly segmented; two thoracic appendages. *Cypris, Cythere, Cypridina, Halocypris.*

3. Order *Copepoda.*—Without shell; five pairs of thoracic limbs; many forms parasitic and degenerate.

1. Suborder *Eucopepoda.*—First thoracic segment only fused with head; abdomen cylindrical and segmented except in highly degenerated forms. *Cyclops, Canthocamptus, Harpacticus, Calanus, Cetochilus* (free-swimming); *Notodelphys* (commensalistic); *Corycæus, Sapphirina, Ergasilus, Caligus, Pandarus* (partly parasitic); *Philichthys, Penella, Lernæa, Chondracanthus, Achtheres, Anchorella* (parasitic).

2. Suborder *Branchiura.*—All thoracic segments fused with head; abdomen small and lamellar, partly parasitic. *Argulus.*

4. Order *Cirrhipedia.*—Sessile or parasitic; segmentation indistinct; six pairs of thoracic appendages; pass through Cypris stage. *Lepas, Scalpellum, Ibla, Balanus* (sessile); *Alcippe, Cryptophialus* (boring); *Proteolepas, Sacculina, Laura, Dendrogaster* (parasitic).

II. Class MALACOSTRACA.—Number of segments constant; thoracic segments eight, abdominal seven or eight.

1. Subclass *Leptostraca.* With bivalved shell; abdomen with eight segments. *Nebalia.*

2. Subclass *Thoracostraca.*—With carapace covering the whole or a part of the thorax; abdominal segments seven.
   1. Order *Schizopoda.*—Thorax completely covered; thoracic appendages biramous. *Mysis*, *Euphausia*, *Siriella.*
   2. Order *Cumacea.*—Last four or five thoracic segments not covered by the carapace; eyes sessile or rudimentary. *Diastylis*, *Campylaspis.*
   3. Order *Stomatopoda.*—Last three or four thoracic segments not covered by the carapace; eyes stalked; five maxillipeds. *Squilla*, *Lysiosquilla*, *Gonodactylus.*
   4. Order *Decapoda.* — Thorax completely covered; five posterior appendages uniramous and three maxillipeds; otocysts in antennules.
      1. Suborder *Macrura.*—Abdomen usually well developed. *Sergestes*, *Lucifer*, *Penæus*, *Palæmonetes*, *Alpheus*, *Cambarus*, *Homarus*, *Eupagurus*, *Birgus*, *Hippa.*
      2. Suborder *Brachyura.*—Abdomen small and concealed beneath cephalothorax more or less perfectly. *Porcellana*, *Libinia*, *Callinectes*, *Platyonychus*, *Cancer*, *Pinnotheres*, *Ocypoda*, *Gelasimus*, *Gecarcinus.*
3. Subclass *Arthrostraca.*—No shell or carapace as a rule; with seven (or six) walking-limbs; eyes sessile.
   1. Order *Anisopoda,*—Carapace slightly developed; first two thoracic segments fused with head; branchiæ on anterior maxillæ. *Apseudes*, *Tanais*, *Anthura.*
   2. Order *Isopoda.*—No carapace; first thoracic segment fused with head; body flattened dorso-ventrally; branchiæ on abdominal appendages. *Asellus*, *Oniscus*, *Porcellio*, *Armadillidium*, *Idotea*, *Sphæroma* (free); *Cymothoa*, *Æga*, *Bopyrus*, *Entoniscus* (parasitic).
   3. Order *Amphipoda.*—No carapace, first thoracic segment fused with head; body flattened laterally; branchiæ on thoracic appendages. *Gammarus*, *Orchestia*, *Corophium*, *Cyamus*, *Caprella.*

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APPENDIX TO THE TYPE CRUSTACEA.

Order **Xiphosura.**

The Xiphosura is a group which possesses many Crustacean peculiarities, and also many foreign to that group and more especially characteristic of the Arachnida; consequently it is advisable to consider it as an order by itself, intermediate between the two types.

A single genus, *Limulus* (Fig. 195), with few species constitutes the order, the members of which are popularly known as King-crabs or Horseshoe-crabs. They are large forms measuring a foot or so in diameter, and the body is composed of three portions. The anterior is a broad semicircular cephalothorax (*cp*), prolonged backwards into sharp points at its posterior angles and bearing upon its dorsal surface a pair of compound eyes towards the sides and near the median line two simple eyes. The middle region is the abdomen (*ab*),

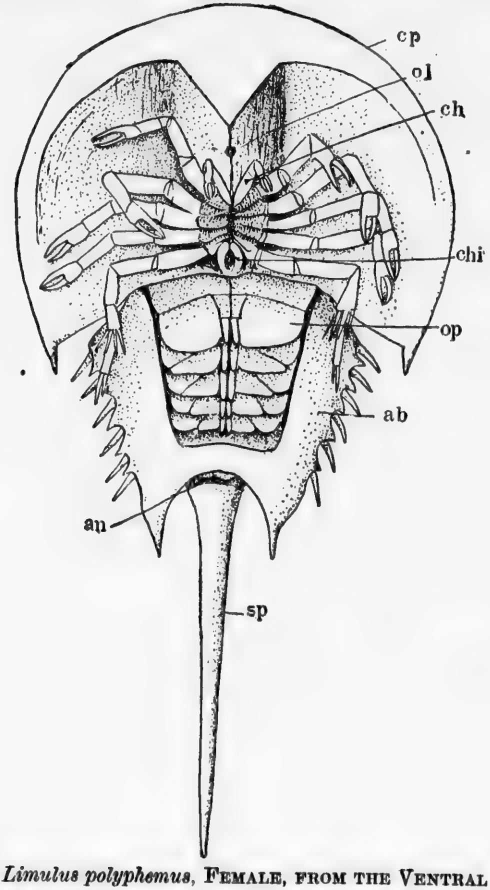

Fig. 195.—*Limulus polyphemus*, **Female, from the Ventral Surface.**

ab = abdomen
an = anus.
ch = chelicera.
chi = chilarium.
cp = cephalothorax,
ol = olfactory organ.
op = operculum.
sp = spine.

showing but faint indication of segmentation, and bearing on its terminal segment the anus, behind which is a long movable spine (*sp*), the post-abdomen, forming the third region and to be regarded probably as a movable prolongation of the dorsum of the last abdominal segment.

The cephalothorax bears seven pairs of appendages. The first pair, the *chelicerœ* (Fig. 195, *ch*), which lie in front of the mouth, are small and, like the following four pairs, are chelate. These together with the sixth are much longer and surround the mouth, their basal joints being provided with strong bristles and serving as jaws. The sixth pair of appendages differ from their predecessors in not being chelate and in possessing upon their basal joints a peculiar process which has been termed the flabellum and by some is regarded as representing an exopodite. The seventh pair of appendages is very different from the others, forming a broad flat plate, the two appendages of the opposite sides meeting in the middle line. This plate covers in the abdominal appendages to a certain extent and hence is termed the *operculum* (*op*). The abdominal appendages, of which there are five pairs, resemble the operculum in form, and like it allow an external larger exopodite and an inner smaller endopodite to be distinguished. They carry upon their posterior surfaces series of large leaf-like, thin-walled folds which function as branchiæ.

The heart (Fig. 196, *ht*) is an elongated tubular organ lying in the posterior part of the cephalothorax and the anterior part of the abdomen, and possesses eight ostia. Arteries arise from it which carry the blood to various parts of the body, eventually, however, opening into the general lacunar system. The blood has a distinct bluish color which deepens on exposure to the air and is due to a copper-containing respiratory pigment, hæmocyanin.

The body is enclosed in a hard chitinous cuticle, and in addition a peculiar fibro-cartilaginous plate, the endosternite, is found in the cephalothorax between the intestine and the nervous system. It is formed by the fusion of a number of tendons and may be regarded as an endoskeleton.

The mouth is an elongated opening lying between the bases of the anterior cephalothoracic appendages and is bounded behind by a pair of processes which represent a lower lip and are known as the *chilaria* (Fig. 195, *chi*). The œsophagus passes upwards and forwards and dilates into a large proventriculus (Fig. 196, *pr*) in the front part of the cephalothoracic shield, and this, bending upon itself and constricting again, opens into the stomach (*s*), from which the intestine (*i*) passes straight back to open on the ventral surface of the body at the base of the terminal spine. The inner wall of the hind-gut, œsophagus, and proventriculus is lined by chitin, which in the last-named structure is thrown into folds and recalls the masticatory apparatus in the stomach of the Decapodous Crustacea. Into the stomach there open the ducts of two pairs of voluminous digestive glands (*l*) which occupy the greater portion of the cephalothorax and are much branched greenish structures.

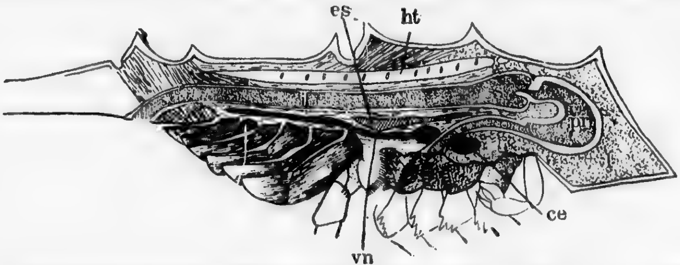

FIG. 196.—LONGITUDINAL SECTION THROUGH A YOUNG *Limulus polyphemus*, DIAGRAMMATIC (after PACKARD).

ce = cerebral ganglion.
es = endosternite.
ht = heart.
i = intestine.
l = liver.
pr = proventriculus.
s = stomach.
vn = ventral nerve-cord.

The nervous system consists of a syncerebrum (*ce*) composed apparently of three pairs of ganglia. It lies in front of the œsophagus, sending branches to the compound and simple eyes. Behind the œsophagus and united with the syncerebrum by circumœsophageal connectives comes a series of seven pairs of ganglia closely approximated, the first pair innervating the cheliceræ and the remaining six the other thoracic limbs in succession. A chain of six pairs of ganglia lying in the abdomen is connected with the cephalothoracic series and innervate the abdominal appendages.

As already noticed, a pair of simple eyes are borne upon the dorsal surface of the carapace, one on each side of the median line, while a pair of larger compound eyes are situated laterally. The structure of these compound eyes is peculiar (Fig. 197). Over their surface the cuticle is considerably thickened and shows upon the outer surface no indication of corneal facets, but its inner surface is prolonged into a number of papillæ (*l*) each one of which projects into a depression of the ectoderm. At the bottom of each depression is a bulblike structure composed of a number of cells arranged in a circle and constituting a retinula (*rt*), the lower ends of the cells being continued inwards to form part of the optic nerves (*opn*). Upon the face which is turned towards its fellow each retinular cell secretes a layer of chitin, and these various chitinous rods being in contact there is formed a structure com parable to the rhabdom of the Crustacean eye. In the centre of the retinular cells and below the rhabdom is a single clear cell (*c*) whose lower end is also prolonged into a nerve-fibre. Each depression with its retinula and the chitinous papilla which fits into it and represents its cornea is an ommatidium, and the development shows that the ommatidia arise as

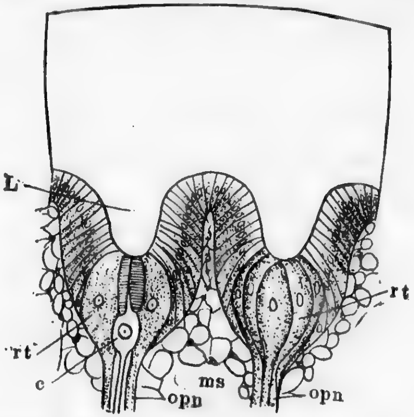

FIG. 197.—COMPOUND EYE OF *Limulus polyphemus*, TWO OMMATIDIA (after WATASE).

c = central cell.
l = lens.
ms = mesoderm.
opn = optic nerve.
rt = retinula.

number of separate invaginations of the ectoderm, the sides of the retinular cells which secrete the rhabdom being in reality those sides which before invagination were at the surface of the body, and the rhabdom may therefore be regarded as composed of portions of the general cuticle which have been separated by the invagination.

On the under surface of the carapace in the median line in front of the cheliceræ is a small tubercle (Fig. 195, *ol*) which contains an organ supposed to be olfactory in function, and probably some of the setæ upon the basal joints of the limbs may also possess a similar function.

Nephridia are represented by a single pair of large reddish bodies lying at the sides of the cephalothorax. Each gland communicates with the exterior at the apex of a papilla situated on the interarticular membrane of the basal joint of the fifth thoracic appendage, and is at first a tubular organ and nephridiumlike, later becoming a lobate and complex structure. Chemical analysis indicates an excretory function for these glands, which have been termed the "brick-red" glands and also the coxal glands, the latter term indicating the situation of their openings on the basal joints (coxæ) of one of the pairs of limbs.

The Xiphosura are bisexual, the genital ducts opening on both males and females on the posterior surface of the operculum near its base. The ovaries are much branched paired structures, the various branches frequently anastomosing even across the median line. The testes are numerous spherical bodies scattered through the body and situated on branching and anastomosing vasa deferentia.

Development and Affinities of the Xiphosura.—When the young *Limulus* leaves the egg it presents a remarkable resemblance to a Trilobite and suggests a possible affinity with these forms which are known to occur only in the Palæozoic rocks. In these same rocks there occur also the remains of forms known as the *Eurypteridæ* which seem to have been even more nearly related to *Limulus* than were the Trilobites. In them the cephalothorax bore apparently only six pairs of appendages which resembled more or less closely those of *Limulus*, except that the sixth pair was broad and oarlike, probably serving for swimming. The abdomen was composed of twelve segments, the anterior six of which were much more massive than the others and bore five pairs of platelike appendages on whose posterior surface were the branchiæ. The terminal segment bore a spine or finlike structure. Such a form as this, represented by the genus *Pterygotus* (Fig. 198), presents strong similarities to *Limulus* and also to the Scorpions, bearing out the numerous similarities of structure occurring between *Limulus* and those forms. This side of the affinity may be postponed, however, until the next chapter, and the comparison of *Limulus* with the Crustacea discussed here. Its chitinous cuticle, its jointed and biramous appendages, and its branchial respiration show similarities to the Crustacea, as do also the form of the heart and the compound eyes. Whether or not the coxal gland is comparable to the shell-gland is at present uncertain, but the other similarities are sufficient to justify the recognition of a Crustacean origin for *Limulus*. It forms indeed a connecting link between the Crustacea and the Arachnida, presenting probably on the whole more affinities with this latter group than with the former.

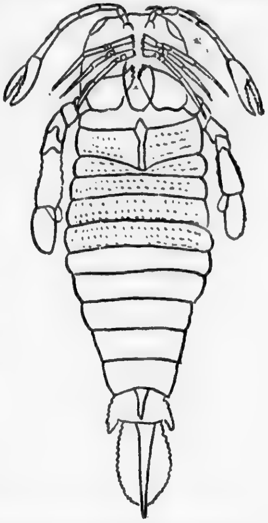
FIG. 198.—*Pterygotus anglicus* (from NICHOLSON).

Since, however, a Crustacean ancestry is probable, a comparision of the appendages of *Limulus* with those of a representative of the ancestral group ought to be possible. It has already been noticed that the brain of *Limulus* is a syncerebrum composed of three segments; it represents, therefore, two segments of which the appendages and other parts have disappeared. Furthermore, recalling that, in the higher Crustacea at least, a ganglion occurring between the cerebral antennary ganglia in the embryo indicates a lost pair of appendages in these forms, the following table may represent the homologies of the appendages of the two groups.

	Crustacean.	Limulus.
1 segment	no appendage	no appendage
2 “	“ “	“ “
3 “	antennules	“ “
4 “	antennæ	cheliceræ
5 “	mandibles	1st pair of legs
6 “	1st maxillæ	2d “ “ “
7 “	2d “	3d “ “ “
8 “	1st thoracic appendages	4th “ “ “
9 “	2d “ “	5th “ “ “
10 “	3d “ “	operculum

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CHAPTER XIV.

TYPE ARACHNIDA.

The Arachnida are essentially terrestrial forms, for though a few species lead an aquatic or marine life, they are evidently descendants of forms which led a terrestrial existence and have only secondarily acquired the power of living under water. In all members of the group the body is covered by a more or less thick chitinous cuticle and the appendages are as a rule jointed.

A characteristic feature of the group is the fusion of the head and thorax to form an unsegmented cephalothorax bearing usually six pairs of limbs. The first pair of these are the *chelicerœ* (Fig. 201, *ch*), composed of one to three joints and terminated either by a claw or a chela; they lie in front of the mouth, which is bounded at the sides by the basal joints of the second pair of appendages, the *pedipalps* (*pe*), which may be long and limblike, or chelate, or in some cases clawlike, their basal joints serving in all cases as mandibles. Behind these follow four pairs of legs composed of six or seven joints, the basal joint being termed the *coxa*, the next, usually short, the *trochanter*, the third the *femur*, the next two together form the *tibia*, then follows in some forms a *metatarsus*, while the terminal one, provided with two claws, termed *ungues*, and in some mites also with a suctorial disk, constitutes the *tarsus*. Variations from this structure of course occur, the chelicerœ, for example, in some mites being reduced to short stylets, and in others the two posterior pairs of legs may be quite rudimentary (*Phytoptus*). The most important variation is, however, that found in the members of the order Solifugæ, in which a head is distinctly marked off from a thorax composed of three segments.

The abdomen in some forms is segmented, in others all trace of the segmentation is lost, and, finally, in the Mites it may be united with the cephalothorax. In the Scorpions it is divisible into an anterior portion, the præabdomen, much broader and stouter than the posterior postabdomen, an arrangement also indicated in certain other forms. In the adults the abdomen is usually destitute of appendages, though they may be present in the embryos; the Scorpions, however, possess two highly-modified pairs, and it seems probable that the four or six papillæ upon which the ducts of the spinning-glands open in the Spiders represent also modified appendages.

A special respiratory system is entirely wanting in a few forms. In the majority there occur on the sides of the body from one to four pairs of pores termed *stigmata* (Fig. 201, st^{1-4}). In the Scorpions and some other forms each stigma opens into a cavity lined with chitin continuous with that which covers the general surface of the body, and into this cavity there project a number of lamellæ arranged like the leaves of a book (Fig. 199), whence the term lung-books frequently applied to them. Each lamella is hollow, trabeculæ extending across the cavity from one wall to the other, and the cavities communicate with the cœlomic lacunæ, so that blood can readily flow into them and so change its gases through the thin walls of the lamellæ. In other cases there occurs in connection with the lung-book apparatus, or else entirely replacing it, a tracheal system consisting of a number of tubes ramifying through the body. In some cases a strong tube or trachea arises at each stigma and traverses the body, giving off branches to all parts as it goes; in others there is in connection with each stigma

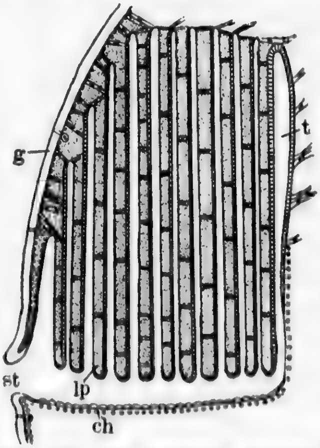

FIG. 199.—TRANSVERSE SECTION THROUGH THE LUNG-BOOK OF A SPIDER (after MCLEOD).

ch = chitinogenous tissue.
g = body-wall.
lp = pulmonary lamella.
st = stigma.
t = last compartment of lung-book, trachealike in character.

a bunch of unbranched tracheæ, and all gradations between these two conditions occur. The tracheæ are lined with chitin, which is sometimes thickened to form rings or spiral bands which serve to keep the lumen of the tubes open and thus permit a free passage of air into them.

The cœlom is filled for the most part with the various organs and is reduced to a series of lacunar spaces containing blood, sometimes rich in hæmocyanin and assuming a blue color when oxygenated. A heart is wanting in some Mites, but is present in the majority of forms, varying from a saclike organ with a single pair of ostia guarded by valves to an elongated cylinder with as many as eight pairs of ostia (Scorpions). It is for the most part situated in the abdominal region, and in the Spiders is enclosed within a space with definite walls which is termed the pericardium, though it cannot be considered homologous with the pericardium of the Mollusca, since it contains blood; muscle-bands extend from it to the walls of the body and by their contraction cause its expansion, fibres in its wall diminishing its cavity and forcing the blood through the ostia into the heart. Arteries in many forms arise from the heart, but after usually a short course open into the lacunar cœlom.

The digestive tract pursues a more or less straight course through the body, but shows a tendency to develop cœcal outgrowths which sometimes reach a considerable size. The anterior and posterior portions of the tract are ectodermal, while the middle region or mid-gut is endodermal and is the portion with which the cœca are connected. In the Scorpions the ducts of a digestive gland open into the mid-gut, and in many forms there is connected with the posterior portion of this same region a pair of tubular Malpighian vessels which are presumably excretory in function and recall the similar structures of the Amphipoda. The end-gut is frequently dilated into a large bladderlike structure, the rectal bladder.

The nervous system consists of a supraœsophageal syncerebrum composed of three pairs of ganglia fused together, and in some forms even four pairs may be included, since the chelicerræ may be innervated from the mass, their ganglia in embryonic life being, however, distinct and postoral in position, only later moving forward. The succeeding ganglia are generally more or less fused, and indeed in some forms all the ganglia of the limb-bearing segments of the cephalothorax may be united with those of the abdominal region to form a single ganglionic mass. In some forms a single ganglion occurs behind this mass at the junction of the cephalothorax and the abdomen, and in the Scorpions there is posteriorly a ventral nerve-cord with seven pairs of ganglia, the anterior pair corresponding with the fifth abdominal segment. A sympathetic nervous system occurs in the Scorpions, Spiders, and Harvest-spiders, consisting of a nerve arising from the syncerebrum and passing to the digestive tract.

Hairs situated upon the body and appendages serve as sense-organs of touch and apparently also of audition, since Spiders are sensitive to air-vibrations and possess no definite auditory organs. Eyes are very generally present and vary considerably in number, there being in the Spiders three or four pairs; in the Scorpions, in which there are from two to six pairs, one pair become closely approximated on each side of the mid-line and recall the median eyes of *Limulus*, while the remaining pairs are situated more to the sides of the cephalothorax. In structure the median eyes differ from the lateral ones; the chitinous cuticle is thickened over them to form a simple unfaceted lens below which lies a layer of transparent cells continuous with the general ectoderm (hypodermis) of the body and which may be termed the corneal hypodermis, though more usually they are known as the vitreous cells. Below them comes the retina, consisting of a single layer of elongated cells with their nuclei situated toward their inner ends, with which the fibres of the optic nerve come into connection. The various retinal cells are arranged in groups of five (retinulæ), which secrete a thin chitinous rod upon their contiguous faces, producing thus a rhabdom composed of five parts. Behind the retina is a thin layer of cells, the postretinular layer, and numerous pigment-cells occur between the various retinulæ. The lateral eyes are constructed upon a very different plan, lacking a corneal hypodermis between the retina and the cornea. They are cup-shaped structures, the cavity of the cup being filled by the cuticular cornea and its wall transformed into the retina, which is continuous at the margins of the cup with the general hypodermis. The retinal cells are of two kinds, viz., large sensory cells and smaller interstitial cells. Each sensory cell is surrounded by pigment and bears upon its lateral walls a chitinous secretion which, with the corresponding secretion of contiguous cells, forms a rhabdom. The nuclei of the cells are situated nearer their inner than their outer ends, and behind them in *Euscorpius* highly refractive spheres occur imbedded in the cells, constituting what have been termed the phaospheres. Upon its inner wall the retina is lined by a basement-membrane continuous with that lying below the general hypodermis and perforated by the fibres of the optic nerves which come into contact with the inner ends of the sensory cells.

In the Spiders, in which there are six or eight eyes arranged upon the dorsum and sides of the cephalothorax, the anterior dorsal pair differs in structure from the remaining ones. In both forms of eyes (Fig. 200) the cuticular cornea (*c*) rests upon a corneal hypodermis, (the vitreous cells, *v*), but the arrangement of the retina differs greatly. In the anterior dorsal pair (*A*) it is composed of a layer of elongated cells (*r*) whose nuclei are situated towards their inner ends, while near

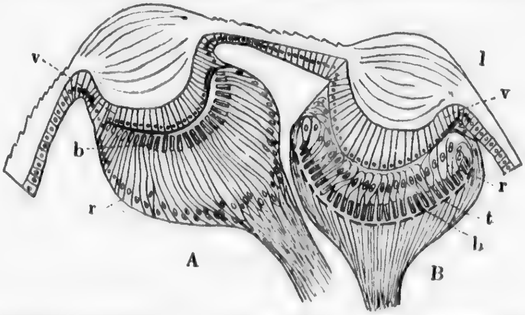

FIG. 200.—EYES OF SPIDER. *A*, ANTERIOR, AND *B*, POSTERIOR EYE (after BERTKAU from KORSCHELT and HEIDER).

b = rods.
r = retina.
l = lens.
t = tapetum lucidum.
v = vitreous layer.

the outer ends are situated a number of rodlike bodies (rhabdoms, *b*), whence these eyes have been termed prebacillar; the nerve-fibres are continuous with the inner ends of the cells. In the posterior dorsal and lateral eyes (*B*) an inversion of the retina (*r*) has taken place, so that the rods (*b*) are situated at the apparently inner ends of the cells and the nuclei at their outer ends, whence the term postbacillar applied to these eyes. The optic nerve-fibres enter at the sides of the eye and are distributed to the nuclear ends of the retinal cells, recalling the arrangement occurring in *Pecten* among the Mollusca. The innermost layer of the eye upon which the ends of the rods rest is cellular, numerous minute crystals being deposited in the cells, whence it has the function of a reflector and is termed the *tapetum* (*t*). It is quite wanting in the prebacillar eyes.

The significance of the structure of the Arachnid eye may be understood by supposing it to have been derived from a compound eye similar to that of *Limulus* (see p. 431), the individualities of the various ommatidia being more or less subordinated. The cuticular cornea in *Limulus* is smooth upon its outer surface, the inner surface being produced into papillæ, one of which corresponds to each ommatidium. In the Arachnids even these papillæ are wanting, the cornea showing no evidence of the presence of ommatidia. The lateral eyes of the Scorpions approach more nearly in their general structure the eyes of *Limulus*, though the condensation of the ommatidia has been carried further than in the median eyes of that form, or in the posterior dorsal and lateral eyes of the Spiders. But in these eyes the condensation is associated with an invagination of the entire eye, a process which, it may be remarked, is indicated in the median eyes of *Limulus*. This invagination has been regarded as a pushing in, under and parallel to the hypodermis, of a pouch of that layer, a process which gives in cross-section the appearance of an S-shaped fold. The outermost layer of the fold forms the vitreous cells or corneal hypodermis, the middle layer the retina, the inversion of which is plainly seen in the posterior dorsal and lateral eyes of the Spiders, while the innermost layer forms the postretinal layer in the Scorpions and the tapetum of the Spiders. The ommatidial retinulæ are more or less retained in these eyes, as is shown by the structure of the rhabdom, which in the Scorpions is composed of five parts, in the Spiders of two, and in the Harvest-spiders of three. The anterior dorsal eyes of the Spiders do not seem to have undergone an invagination, hence the absence of a tapetum and the prebacillar structure of the retina; a corneal hypodermis is, however, present, and would seem to indicate an invagination, but its mode of origin seems at present but imperfectly understood. If a generalization is to be made, it will be to the effect that the eyes of the Arachnids have been derived from compound eyes similar to those of *Limulus*, and that in the median eyes of the Scorpions, and the posterior dorsal and lateral eyes of the Spiders the entire optic area has been invaginated, making them comparable to the median eyes of *Limulus*, while the lateral eyes of the Scorpions and the anterior dorsal eyes of the Spiders have not undergone invagination and hence are comparable to the lateral eyes of *Limulus*. Whether the comparability indicates also the homology from a phylogenetic standpoint of eye to eye must remain at present uncertain (see p. 457).

In addition to the Malpighian tubules already mentioned as excretory organs occurring in connection with the digestive tract of the Spiders, there exist in many forms additional glands which probably are also excretory in function or significance. These are the coxal glands, so called on account of their openings when present being on the basal joints (coxæ) of one of the pairs of legs. In the Scorpions and Spiders the ducts of the glands open on the third pair of legs (i.e., the fifth pair of appendages) in the embryo, but are usually wanting in the adults. In the Solifugæ and Harvest-spiders coxal glands also occur in connection with the fourth pair of legs, and similar glands have also been observed in several genera of Mites, opening, however, at varying points.

Glands are also of frequent occurrence in connection with the pedipalps, having apparently varying functions in different genera. They do not, however, seem to belong to the same category as the coxal glands and are in no case excretory.

The Arachnida are bisexual throughout. The ovaries not infrequently fuse to form a single mass or a circular band, and in connection with the oviducts, which are in direct communication with them, there is usually developed a receptaculum seminis, and in the Harvest-spiders, an elongated ovipositor. The testes are also frequently fused, and the vasa deferentia are provided with vesiculæ seminales and usually terminate in a copulatory organ. The majority of forms are oviparous, exceptions to the rule being found, however, as in the genus *Phrynus* and in the Scorpions, which are viviparous.

1. Order **Scorpionida.**

In the Scorpions (Fig. 201) the body is composed of an unsegmented cephalothorax and an elongated segmented abdomen. The seven anterior segments (the præabdomen) of the abdomen are broader and thicker than the remaining five segments (the postabdomen), the last one of which terminates in a curved stout spine which bears at its extremity the openings of two ducts leading from a pair of glands lying in the twelfth abdominal segment and secreting a poisonous fluid.

The cheliceræ (*ch*) are small chelate appendages situated in front of the mouth, while the pedipalps (*pe*) are long and provided with strong chelæ, their basal joints and those of the two succeeding appendages surrounding the mouth and serving as jaws. The four pairs of appendages behind the pedipalps are all similar in form, being six-jointed walking-limbs. Upon the abdomen modified appendages are also found, the second abdominal segment bearing a pair, each member of which consists of a single joint whose posterior edge is beset with a number of processes which give it the appearance of a comb, whence the name pectines (*pt*) applied to these appendages. In front of the pectines lies the genital opening, protected by a small genital operculum (*op*) which may possibly represent another pair of appendages belonging to the first abdominal segment.

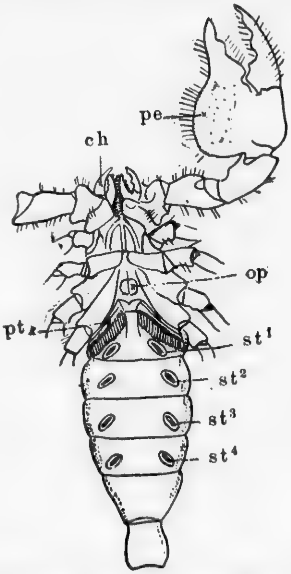

FIG. 201.—SCORPION (after OWEN).
ch = cheliceræ.
op = genital operculum.
pe = pedipalp.
pt = pecten.
st^{1-4} = stigmata.

Upon the ventral surfaces of third, fourth, fifth, and sixth abdominal segments elongated pores are to be found which are stigmata (st^{1-4}) leading into the respiratory cavities containing the lung-books, of which there are in all four pairs in this group. No tracheæ occur.

The intestine is quite straight in the Scorpions and lacks cæcal outgrowths excepting the two Malpighian tubules situated at the posterior end of the mid-gut. The digestive gland is a large five-lobed structure which empties through several ducts into the mid-gut.

The nervous system consists of a syncerebrum lying above the œsophagus and giving rise to nerves for the eyes and for the cheliceræ. It is connected with a subœsophageal mass from which the pedipalps and the three anterior legs are innervated, the fourth pair of legs receiving its nerves from a pair of distinct ganglia separated only by a short distance from the subœsophageal mass. Behind this in the abdomen is a chain consisting of seven pairs of ganglia united by long connectives. The eyes vary in number from two to six pairs, one pair being situated on or near the median line, while the others are lateral.

Coxal glands occur in connection with the third pair of legs, and the heart is an elongated structure lying in the anterior portion of the abdomen and possessing eight pairs of ostia.

The Scorpions are viviparous. The ovaries are situated in the anterior abdominal region and are elongated, that of one side of the body being united with the other by several transverse connections. The oviducts, which are short, serve as uteri, and open to the exterior by a single median opening situated on the ventral surface of the first abdominal segment. The testes consist of four tubes, those of the same side being connected by transverse anastomoses, and unite together to open into a protrusible penis, accessory glands, vesiculæ seminales, occurring in connection with each vas deferens. The single genital orifice occupies the same position as in the female.

The Scorpions are confined to the warmer regions of the globe, but few genera being known. Of these the genera *Euscorpius* and *Buthus* are perhaps the commonest.

2. Order **Pseudoscorpionida.**

This order includes a number of small forms which are found under the bark of trees or among dead leaves or moss, one genus, *Chelifer* (Fig. 202), occurring occasionally between the pages of books, and hence being known popularly as the Book-scorpion. The cephalothorax is unsegmented, and is followed by a broad flattened abdomen composed of eleven segments. A præabdomen and a postabdomen, such as can be distinguished in the Scorpionida, does not occur, nor is there a terminal poison-spine nor a poison-gland.

The chelicerae and pedipalps resemble those of the Scorpions, being chelate, and the four succeeding appendages are walking-legs, while the abdomen possesses no appendages in the adult. Both the second and third abdominal segments bear upon their ventral surfaces a pair of stigmata which are the openings of tubular tracheæ which extend through the body sending off branches, except in *Chernes*, in which bunches of unbranched tracheæ arise from each stigma. A heart is present, but consists of a simple tube with either a single pair of ostia near its posterior extremity (*Obisium*) or with four ostia (*Chernes*).

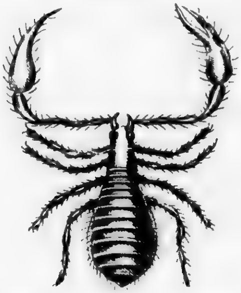
FIG. 202.—*Chelifer carcinoides* (from CUVIER).

The endodermal portion of the digestive tract gives rise to a pair of lateral cæcal diverticula branched at the apex and to one unpaired ventral one. Two eyes are present in *Chelifer* and four in *Obisium*, while they are entirely wanting in *Chernes*. The reproductive organs open upon the ventral surface of the second abdominal segment, and the opening is surrounded with glands which secrete a fluid which quickly hardens to silky filaments and serves to fasten the eggs to the abdomen of the parent. These glands are hypodermal in origin and correspond to the spinning-glands of the Spiders.

3. Order **Solifugæ.**

The members of this order are characterized by the head-region being separated from a thorax consisting of three segments and bearing the three posterior pairs of legs. The abdomen is also segmented, its ten segments showing no differentiation into præabdomen and postabdomen, nor does it possess any sting or poison-gland. The chelicerae are chelate, but the pedipalps are long and leglike and possess glands which in *Galeodes* have been supposed to be poisonous. The anterior pair of legs lacks the terminal ungues found on the others, and functions as a second pedipalp rather than a walking-leg. No appendages occur on the abdomen.

Three pairs of stigmata occur on the ventral surface of the body, the most anterior pair being situated on the first thoracic segment, while the other two are on the second and third abdominal segments. The anterior position of the first pair is probably to be regarded as secondary, and produced by a forward migration of the pair which should occur upon the first abdominal segment. The stigmata lead into tubular tracheae which branch extensively. A comparatively simple heart is situated in the abdomen.

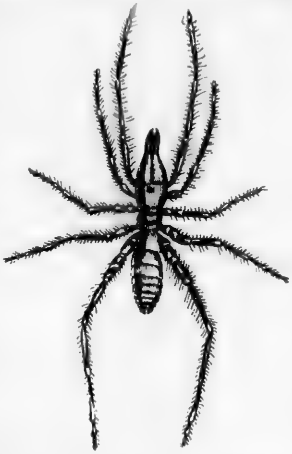

FIG. 203.—*Galeodes spinipalpus* (from CUVIER).

The mid-gut possesses numerous branched diverticula as well as Malpighian tubules. The nervous system consists of a syncerebrum connected with a subœsophageal mass which represents all the thoracic and abdominal ganglia fused together. Two eyes are present, situated on a common elevation at the front edge of the head.

The reproductive organs resemble those of the Scorpions except that transverse anastomoses do not occur, and the genital opening is situated upon the ventral surface of the first abdominal segment.

The Solifugæ is a small order living more especially in warm sandy regions. They are usually, on rather insufficient grounds, supposed to be capable of inflicting a poisoned wound. Only two genera, *Solpuga* and *Galeodes*, belong to the order.

4. Order **Pedipalpi.**

The order Pedipalpi includes two genera, *Phrynus* and *Thelyphonus*, both of which are inhabitants of the warmer regions of the earth. The cephalothorax is unsegmented; the abdomen in *Phrynus* is elongated and oval, and composed of eleven segments showing little differentiation of form, while in *Thelyphonus* there are twelve segments, the last three of which are much smaller than the others and bear a long, many-jointed terminal filament. The cheliceræ are not chelate, but the terminal joint may be flexed upon the basal one and contains the duct of a poison-gland which opens at its extremity. The pedipalps in *Phrynus* are long and leglike, though richly provided with spines, and terminate with ungues, but in *Thelyphonus* they are relatively short and stout with a flexible terminal joint as in the chelicerae; in both genera the basal joints of the two pedipalps are fused. The first leg is long and slender and terminates in a filament-like structure, the other three pairs being typical walking-legs.

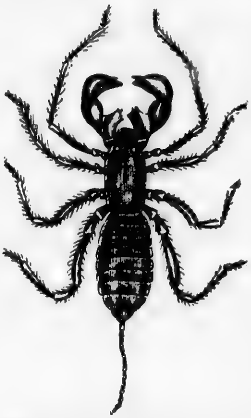

FIG. 204.—*Thelyphonus caudatus* (from CUVIER).

Four stigmata occur, one pair situated in the second and another in the third abdominal segment, and they open into cavities containing lung-books. The digestive tract is comparatively simple, but the nervous system shows a concentration of the postœsophageal ganglia similar to that described for the Solifugæ, except that a single pair of ganglia occurs in the abominal region united by long connectives with the cephalothoracic mass. Eight eyes are present, two of which are larger than the others and situated at the anterior edge of the dorsal surface of the cephalothorax, while the other three pairs are situated laterally.

The reproductive organs are paired and open by a median orifice situated on the ventral surface of the first abdominal segment. *Phrynus* is viviparous.

5. Order **Phalangida.**

The Phalangida (Fig. 205), popularly known as the Harvest spiders, possess an unsegmented cephalothorax (*ct*) and have from six to nine segments composing the abdomen (*ab*). The cheliceræ are chelate, while the pedipalps (*pe*) are long and leglike, with terminal ungues. The eight walking-legs are usually exceedingly long, though in the genera *Cyphophthalmus* and *Gibbocellum* they are shorter. A single pair of stigmata are usually all that occur; they are situated upon the first abdominal segment and open into branching tracheæ. In *Gibbocellum*, however, two pairs occur, situated upon the second and third abdominal segments, the anterior pair opening into branched tracheæ, while a bunch of simple unbranched tracheæ arises from each of the posterior ones. The heart is somewhat elongated and possesses three pairs of ostia; arteries are entirely wanting, the blood passing from the heart directly into the lacunar spaces.

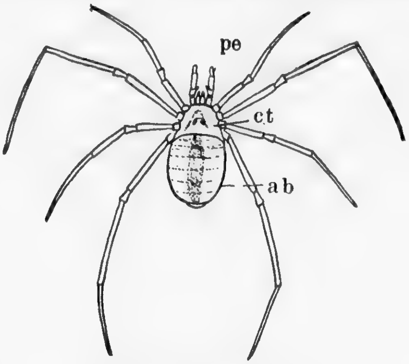

Fig. 205.—*Leiobunum.*

ab = abdomen. *ct* = cephalothorax. *pe* = pedipalps.

The digestive tract dilates into a sac-like stomach from which numerous much-branched cæcal diverticula pass off. Malpighian vessels, two in number, are found in *Cyphophthalmus* and *Gibbocellum*, and have been described as occurring in other forms also, though it is probable that two glandular tubes which open to the exterior on the sides of the cephalothorax have in some forms been mistaken for these organs. Odoriferous glands are also found in the abdomen of some forms, and so-called salivary glands occur in connection with the pedipalps.

The nervous system shows a marked concentration of the postoral ganglia, a single pair only remaining separate from the fused mass formed of the remainder. The majority of forms possess but a single pair of eyes on the dorsum of the cephalothorax, but in *Gibbocellum* two lateral pairs are found.

Coxal glands have been described in connection with the coxal joints of the third pair of legs and have been observed to communicate with the exterior, differing therefore from those of other Arachnoids in being functional in the adult. The reproductive organs are unpaired, a condition which results from the fusion of originally paired structures, and the genital pore lies in both sexes at the junction of the cephalothorax and abdomen or on the first abdominal segment. The vasa deferentia and oviducts are paired, each of the former communicating with a protrusible penis, while similarly each oviduct unites with a long protrusible ovipositor.

Certain genera such as *Leiobunum* (Fig. 205), *Phalangium*, and *Opilio*, are exceedingly common, and to them the terms Harvest-men, Harvest-spiders, or Daddy Longlegs are popularly applied. Other forms, such as *Gonyleptus*, with spinose pedipalps, are tropical in habitat, while *Cyphophthalmus* and *Gibbocellum* have a limited distribution, and on account of the many differences of structure which they present when compared with other forms are sometimes grouped together to form a separate order. It is to be noted especially that these two forms possess upon the second abdominal segment a pair of wartlike elevations at the summit of which the ducts of numerous spinning-glands open.

6. Order **Araneæ**.

The order Araneæ includes a large number of forms possessing very definite characteristics. The cephalothorax is unsegmented, as is also the abdomen, which is an oval, spherical, or sometimes irregularly-shaped region which narrows suddenly anteriorly so as to be much narrower than the cephalothorax. The cheliceræ project somewhat in front of the cephalothorax and each consists of a broad basal joint and a terminal strong claw which may be flexed upon the basal joint, and has opening at its tip the duct of a poison-gland (Fig. 206, *pg*) which lies in the cephalothorax. The pedipalps of the females are leglike structures usually with a terminal unguis, but in the male are more or less swollen to serve as accessory organs in copulation. The four pairs of seven-jointed legs are all similar in structure and serve for walking, differing in relative length in different genera. In the embryo the abdomen is distinctly segmented and bears five or six pairs of rudimentary appendages, the more anterior of which later disappear, while the two or three posterior pairs persist as the spinnerets (*sp*), so called from the occurrence on them of the openings of the ducts of the spinning-glands (*spg*).

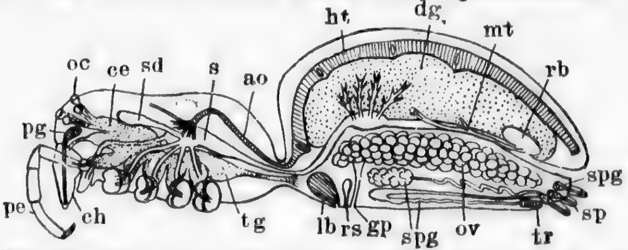

FIG. 206.—DIAGRAM OF STRUCTURE OF A SPIDER (after LEUCKART).

ao = aorta.
ce = cerebral ganglion.
ch = chelicera.
dg = digestive gland.
gp = genital pore.
ht = heart.
lb = lung-book.
mt = Malpighian tubule.
oc = eye.
ov = ovary.
pe = pedipalp.
pg = poison-gland.
rb = rectal bladder.
rs = receptaculum seminis.
s = stomach.
sd = stomach diverticulum.
sp = spinneret.
spg = spinning-glands.
tg = thoracic ganglion.
tr = trachea.

These are very numerous and open at the apices of the spinnerets, each gland producing a fluid secretion which quickly hardens on exposure to the air to form a silken thread. The thickness of the thread may be modified by uniting together the secretions of a greater or less number of the glands, which, moreover, differ among themselves, some producing, for instance, a sticky secretion with which certain of the threads may be covered. In some forms there is situated upon the abdomen just in front of the spinnerets a chitinous plate, the *cribellum*, which is perforated, like the spinnerets, by the ducts of numerous spinning-glands. Its presence is associated with that of a *calamistrum*, a peculiar modification of the metatarsus of the last pair of legs, it being furnished with a double row of bristles which are rapidly waved over the cribellum and draw from its glands their secretion. The threads are used for several purposes, as, for example, to fasten the ova to the body of the parent or to form a cocoon for them, or else to form a snare by which insects may be caught to serve as food. These snares in some cases are composed of an irregular network of threads arranged without any definite pattern, as in *Theridium*, but some other forms show a certain amount of architectural skill, weaving a platform of felted threads which terminates in a tubelike place of concealment for the spider (e.g., *Agelena*, *Tegenaria*) or webs composed of threads radiating from a central point and united by other threads arranged in a spiral or in concentric circles (e.g., *Epeira*, the common garden-spider), or else using the threads to form a hinged trap-door covering in a burrow in the earth which serves as a domicile as in the Trap-door Spider.

The digestive tract expands in the thoracic region into a saclike structure (*s*) from each side of which three or more usually five cæcal diverticula (*sd*) arise, the anterior pair sometimes anastomosing so as to form a ring, while in some cases (*Epeira*) secondary diverticula extend from the more posterior ones into the coxal joints of the legs. In the abdomen the intestine is more cylindrical, giving rise to much-branched lateral diverticula which together form the so-called liver (*dg*), and having connected with it, just as it joins the end-gut, two elongated Malpighian tubules (*mt*). The end-gut itself dilates into a large rectal bladder (*rb*) which a short

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rectum connects with the anus situated at the posterior extremity of the body.

In the genus *Mygale* and allied forms two pairs of stigmata are found near the anterior portion of the abdomen, both of which lead into cavities containing lung-books. In the majority of forms, however, but one pair of lung-books (*lb*) occurs, the second pair of stigmata opening into a tracheal tube (*tr*) extending into the cephalothorax and terminating in a bunch of unbranched tracheæ, a similar bunch arising near its base and extending backwards into the abdomen (*Segestria*). In some forms the second or tracheal stigmata may be situated far back upon the abdomen, and may be united to a single median transversely-elongated cleft, from which a bunch of unbranched (*Attus*) or branched tracheæ arises.

The heart (*ht*), which lies in the abdomen, is enclosed within a so-called pericardium and possesses three pairs of ostia. It is continued anteriorly and posteriorly into aortæ, and gives off also lateral arteries, all of which open after relatively short courses into the lacunar spaces. The blood is returned to the pericardial cavity, whence it passes into the heart, the greater portion on its way to the pericardium passing through the lung-books.

The nervous system consists of a syncerebrum (*ce*) and a large cephalothoracic ganglionic mass (*tg*). In addition to the nerves to the appendages, a posterior nerve arises from this mass and passes backwards towards the abdomen, in *Mygale* dilating at the junction of that region with the cephalothorax into a pair of small ganglia. A sympathetic or visceral system, consisting of a nerve arising by paired trunks from the brain, is distributed to the anterior portion of the digestive tract. The eyes are usually numerous, three or four pairs occurring on the anterior portion of the cephalothorax, their arrangement varying in different genera.

Coxal glands have been found in several forms in connection with the first pair of legs, and in *Mygale* they occur in connection with the third pair. The reproductive organs open in both sexes by a single opening situated near the anterior end of the abdomen between the anterior stigmata. The ovaries (*ov*) are paired, or may unite to form a ring, and the two short oviducts unite to form a vagina with which may be associated receptacula seminis (*rs*), though more usually these structures open independently in front of the genital orifice and may be single, or paired, or in some cases even three in number. The testes are cylindrical structures whose long, slender, and frequently-contorted vasa deferentia unite just before opening to the exterior. A remarkable copulatory organ is formed by the terminal joint of the pedipalp of the male (Fig. 207), which bears upon its inner surface a process containing a spirally-coiled tube. This tube opens at the extremity of the process, and is filled by the spider with spermatozoa, and during copulation is inserted into the receptacula seminis of the female.

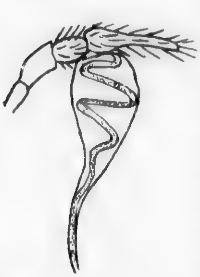

FIG. 207.—PEDIPALP OF MALE SPIDER (after BERTKAU).

The males are usually smaller than the females, and their approaches are frequently resisted by the latter, who endeavor to capture and destroy the persistent swains. In the Attidæ a process of courtship has been observed to occur, the male posturing before the female and displaying to their best advantage the highly-colored hairs with which the body is covered. The ova are in many forms (*Lycosa*) attached to the under surface of the abdomen, while in others they are enclosed in a silken cocoon which may either be carried about by the female or suspended in the webs or deposited in protected situations.

Two suborders are recognized, according as there are two pairs of lung-books or only one. The *Tetrapneumones* include the forms with two pairs of lung-books, among which are the Trap-door Spiders, *Cteniza*, already mentioned, and the Tarantula, *Mygale*, the largest of all the spiders and reputed to attack even small birds. The *Dipneumones* have but a single pair of lung-books, the majority of living spiders belonging to the suborder. Some, such as *Epeira*, *Agelena*, *Tegenaria*, *Theridium*, and *Segestria*, spin webs, while others catch their prey by their rapid movements (*Lycosa*) or by suddenly springing upon it (*Attus*).

7. Order **Acarina.**

The Acarina are for the most part small forms, many being almost microscopic, while the largest, the Ticks (*Ixodes*), do not when at their greatest size exceed a centimeter in length, the males being much smaller. Some forms, such as *Oribates* and *Nothrus*, live among moss and in similar situations, while others, such as *Hydrachna* and *Atax*, are aquatic. Many forms are, however, parasitic either upon plants (*Tetranychus* and *Phytoptus*) or on animals, the genus *Sarcoptes* being the cause of the disease termed the Itch in man, the symptoms being produced by the Mites burrowing beneath the skin. Other forms affect various animals and birds, the genera *Dermaleichus*, *Analges*, etc., feeding upon the feathers of various birds, while others, such as *Demodex* (Fig. 208, *B*), live in the hair-follicles or sebaceous glands of the skin, producing acnelike pustules. The larvæ of many forms which are non-parasitic in adult life have a parasitic habit, as for instance the larvæ of many of the Water-mites and of the Harvest-mites (*Trombidium*), while other forms live upon organic matter of various kinds, as does the Cheese-mite, *Tyroglyphus*.

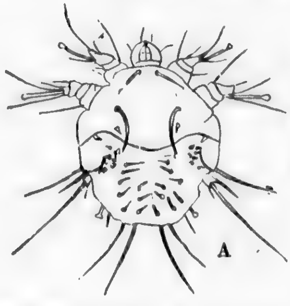

FIG. 208.—*A*, *Sarcoptes scabiei*; *B*, *Demodex phylloides* (after CSOKOR from WRIGHT).

A distinguishing characteristic of the Acarina is the absence of any segmentation and the fusion of head-thorax and abdomen to a single mass (Fig. 208, *A*). The form of the appendages varies greatly in different genera according to the use to which they are put. The cheliceræ (Fig. 209, *Md*) are frequently chelate, but in parasitic forms are reduced to stylets enclosed by the fused basal joints of the pedipalps, a proboscis being thus produced which can pierce the integument and thus render the juices of the host available as food. The pedipalps (*Mxp*) undergo various modifications, being sometimes long and limblike, sometimes chelate, while their basal joints may or may not be fused. The four pairs of legs are generally adapted for walking, and terminate in ungues or bunches of hairs or, in some parasitic forms, in suctorial disks, while in the Water-mites they are provided with usually long bristles along the sides, serviceable swimming-organs being thus produced. In the genus *Demodex* the four legs are reduced to short unjointed structures each provided with four ungues, while in the Leaf-mites, *Phytoptus*, which produce galls on the leaves of various plants, the two pairs of posterior limbs are reduced to wartlike elevations bearing bristles, the two anterior pairs being on the other hand five-jointed.

The chitinous covering of the body is usually thick and delicately wrinkled. It usually bears numerous setæ and occasionally also plates or lateral prolongations, as in *Oribates* and its allies. Dermal glands also frequently occur, producing oily fluids and sometimes odoriferous secretions. Spinning-glands opening on the pedipalps occur in *Tetranychus*, frequently parasitic on the leaves of the Rose, but as a rule they are not developed.

A pair of stigmata (Fig. 209, *st*) occurs in many forms, situated usually near the coxæ of the last pair of legs, but not unfrequently they are much further forward, lying near the basal joints of the pedipalps or even of the cheliceræ. They open into tracheæ which branch once, bunches of lateral tracheæ being situated at intervals upon the two branches. Frequently, however, especially in parasitic and aquatic forms, both tracheæ and stigmata are wanting, as is usually also the heart. When present (*Gamasus*, *Ixodes*) this latter structure is small, with but a single pair of ostia, and is prolonged anteriorly into a slender aorta.

The digestive tract is frequently provided with glands opening into its anterior portion and supposed to be salivary.

The mid-gut usually sends off a number of cæcal diverticula which may branch at the ends, and Malpighian vessels, sometimes one, sometimes a pair, and sometimes many are usually present, while in addition, in some forms, a rectal bladder, similar to that occurring in the Araneæ, is found.

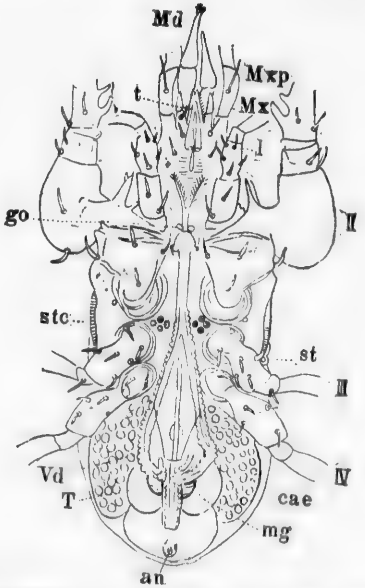

FIG. 209.—MALE OF *Gamasus tergipes* (after WINKLER).

an = anus.
cæ = cæcal pouches of intestine.
go = genital orifice.
Md = chelicera.
mg = Malpighian tubules.
mx = maxillæ.
Mxp = pedipalps.
st = stigma.
stc = stigma-canal.
T = testis.
t = tongue.
Vd = vas deferens.
I–IV = limbs.

The nervous system, as might be supposed from the concentration of the body regions, is composed of a supraœsophgeal syncerebrum and a larger subœsophageal ganglionic mass from which numerous nerves are given off. Eyes are usually wanting, or may be present in the form of one (*Ixodes*) or two pairs of small apparently simple ocelli.

Coxal glands have been described as occurring at the bases of the second pair of legs (Oribatidæ). The reproductive organs show much variety in their arrangement, being sometimes paired and sometimes united to a single mass. The single genital orifice is situated far forward, in some cases even between the basal joints of the second pair of legs. Numerous accessory structures may be associated with the ducts, the receptacula seminis in some forms opening to the exterior quite independently of the oviduct, and protrusible organs serving for copulation in the male and for oviposition in the female may occur. The Acarina are as a rule oviparous, though a few forms are viviparous.

Development of the Acarina.—Most of the Acarina whose development has been traced pass through a series of larval stages. While the young embryo is still within the egg and sometimes before the appendages have developed, a cuticular membrane is secreted around it lying between the embryo and the egg-shell. This is the *deutovum*, and within it further development proceeds. In those forms in which it does not appear until after the appendages are formed a degeneration of these structures takes place, and the egg-shell may also be thrown off leaving the embryo surrounded only by the deutovum (*Trombidium*). New appendages now appear, and the larva hatches out from the deutovum as a six-legged form, sometimes showing traces of segmentation either in the thoracic region or in the abdomen. After a certain time a certain amount of degeneration of the tissues occurs (histolysis) and the appendages again disappear, a chitinous membrane forming around the now almost spherical body of the larva. A regeneration of the limbs and tissues takes place within this larval membrane, and the nymph is formed, resembling the adult in the number of appendages, but lacking fully-developed reproductive organs. A period of rest, and histolysis again occurs, accompanied by the formation of a third cuticular membrane within which the nymph becomes transformed into the fully-developed and sexually-mature adult or imago, which finally issues from the membrane.

This complicated process, it is needless to say, has no phylogenetic significance, the deutovum indeed being absent in certain forms (*Tetranychus*), nor does it seem likely that even the six-legged larva is anything but a secondary stage which has been developed within the group of the Acarina. There is no question but that the order represents the culmination of a divergent line of evolution, perhaps from the Pseudoscorpionida, and since the separation many of the peculiarities characteristic of the group have been developed.

Phylogeny of the Arachnida.—There seems little room for doubt but that the Scorpions among living forms represent most closely the ancestral Arachnoids, their segmentation being most perfect and their appendages more numerous than those of other forms. It is through the Scorpions accordingly, that relationships to other forms must be looked for, and a comparison of them with *Limulus* reveals similarities of structures so numerous and so detailed that the conclusion is unavoidable that both are to be traced back to a common ancestor. Thus the cephalothoracic appendages in both are identical in number, and, so far as the first two pairs are concerned, in general structure also, while the genital opercula of the Scorpions are comparable in their relation to the genital orifices to the opercula of *Limulus*, and the pectines to the first pair of abdominal appendages. The remaining abdominal appendages of *Limulus*, which are branchiate, seem at first sight to be unrepresented, but the embryological investigation of the Scorpions appears to indicate that they are represented by the lung-books, which bear no little resemblance to the branchial lamellæ of *Limulus*, and the conversion of one set of organs into the other may be supposed to have been brought about by the formation behind each pair of abdominal appendages of an invagination, which, deepening, has carried in with it the branchial lamellæ, the original anterior surface of the appendage forming the ventral wall of the body beneath the lung-sac, while the lamellæ project into the sac for its ventral surface (Fig. 210). In the general form of the body *Limulus* corresponds fairly well with the Scorpions, the cephalothoracic regions being strictly comparable, as is also the terminal spine with the sting; the abdomen, however, in the branchiate form has a smaller number of segments which are all fused, a difference readily explained by the probable derivation of both forms from *Eurypterus*-like ancestors in which the abdomen possessed a relatively large number of distinct segments, and even showed indications of a differentiation into a præabdomen and a postabdomen (see Fig. 198).

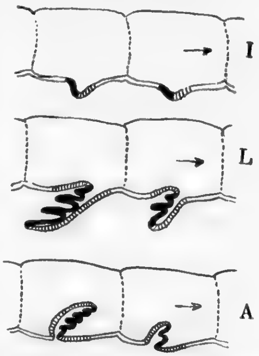

FIG. 210.—DIAGRAM OF ORIGIN OF LUNG-BOOKS (after KINGSLEY).

I = indifferent stage.
L = Limulus stage.
A = Arachnidan stage.

In the internal structure quite as striking similarities are to be found in the presence of an endosternite in both groups and of coxal glands in connection with the fifth pair of appendages, in the tendency towards the concentration of the postoral ganglia, and in the invaginate origin of the median eyes, to mention but a few points.

The Arachnida are accordingly to be traced back to *Limulus* or *Eurypterus*-like ancestors, and through these finally to the Entomostraca, perhaps, a Crustacean ancestry being clearly indicated. As to the relationships of the various orders little that is definite can be said, differentiations having taken place along different lines in the various orders, so that while the

Pedipalpi are more primitive as regards the number of abdominal segments and their distinctness than the Araneæ, yet the latter and especially the Tetrapneumones show a much more primitive condition of the respiratory organs. With regard to these organs it may be stated that the condition in which they are represented by bunches of unbranched tracheæ is more primitive than that in which they are branching tubes, the bunched condition being probably derived by a modification of original lung-books.

TYPE ARACHNIDA.

1. Order *Scorpionida.*—Abdomen segmented and differentiated into præabdomen and postabdomen ; postabdomen terminating in poison-spine ; pedipalps chelate ; two pairs of abdominal appendages ; four of stigmata and lung-books. *Euscorpius*, *Buthus.*
2. Order *Pseudoscorpionida.*—Abdomen segmented but not differentiated ; no terminal spine ; pedipalps chelate ; no abdominal appendages ; two pairs of stigmata opening into tracheæ : first pair of legs adapted for locomotion. *Chelifer*, *Obisium*, *Chernes.*
3. Order *Solifugæ.*—Head separated from thorax with three segments ; abdomen segmented but undifferentiated ; no terminal spine ; pedipalps palplike ; three pairs of stigmata leading into tracheæ. *Galeodes*, *Solpuga.*
4. Order *Pedipalpi.*—No distinction of head and thorax ; abdomen segmented, and either undifferentiated or with three small segments terminated by a multiarticulate flagellum ; pedipalps leglike or subchelate ; two pairs of stigmata and lung-books ; first pair of legs elongated and palplike. *Phrynus*, *Thelyphonus.*
5. Order *Phalangida.*—Abdomen segmented but undifferentiated and without appendages or terminal spine ; pedipalps leglike ; one pair of stigmata leading into tracheæ ; no spinning-glands. *Leiobunum*, *Phalangium*, *Opilio*, *Gonyleptus*, *Cyphophthalmus*, *Gibbocellum.*
6. Order *Araneæ.*—Abdomen unsegmented and with two or three pairs of rudimentary papillalike appendages bearing the openings of ducts of numerous spinning-glands ; abdomen not fused with cephalothorax ; pedipalps long and palplike or leglike.
    1. Suborder *Tetrapneumones.* — With four stigmata opening into sacs containing lung-books. *Mygale*, *Cteniza.*
    2. Suborder *Dipneumones.*—With four or three stigmata, the anterior pair opening into sacs with lung-books, the posterior one or two with tracheæ. *Epeira*, *Agelena*, *Tegenaria*, *Theridium*, *Segestria*, *Attus*, *Lycosa.*
7. Order *Acarina.* — Abdomen unsegmented, without appendages, and fused with the cephalothorax ; pedipalps sometimes long and leglike, sometimes chelate ; stigmata wanting or present as a

single pair leading into tracheæ; many forms parasitic; frequently with complicated metamorphoses.

Nonparasitic, or parasitic only in larval stage; terrestrial. *Oribates*, *Nothrus*, *Trombidium*.

Aquatic. *Hydrachna*, *Atax*.

Living on organic matter. *Tyroglyphus*.

Parasitic on animals. *Demodex*, *Sarcoptes*, *Dermaleichus*, *Analges*, *Gamasus*, *Ixodes*.

Parasitic on plants. *Tetranychus*, *Phytoptus*.

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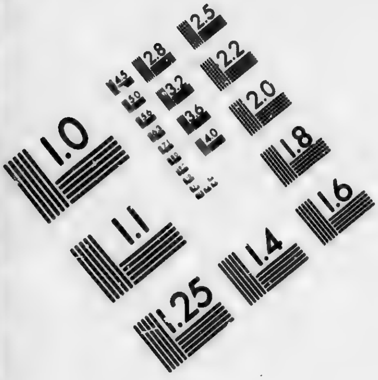
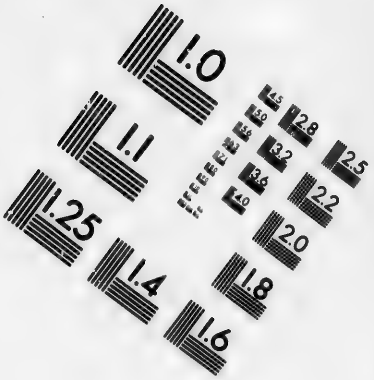

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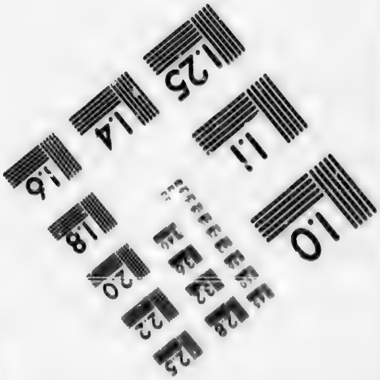

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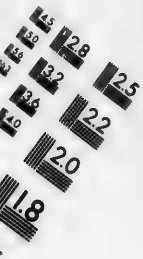
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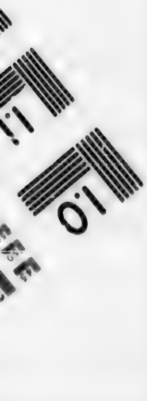
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APPENDIX TO THE ARACHNIDA.

There are three orders which show a certain amount of affinity to the Arachnida, but which are not so closely related as to warrant the actual association of them with the orders which have been assigned to that type. They will be described here, and are the orders of the *Pentastomidæ*, the *Pycnogonida*, and the *Tardigrada.*

Order **Pentastomidæ.**

The Pentastomidæ are all parasitic, living in the adult stage in the lungs or nasal cavities of various animals, one species, *Pentastomum tænioides*, occurring in the nasal cavities or sinuses of dogs and wolves, while several species have been found in the lungs of different species of snakes (Fig. 211). They are all elongated wormlike forms, sometimes slightly flattened and usually distinctly annulated, the annuli, however, not representing a metamerism. The anterior end of the body is rounded and bears on the ventral surface the mouth, upon each side of which is situated a pair of strongly-recurved hooks (*h*) supplied with special muscles and serving for the attachment of the animal to the tissues of the host. With the exception of these hooks no appendages are present.

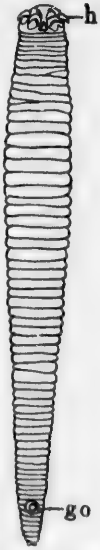

FIG. 211.—*Pentastomum teretiusculum*, FEMALE (after SPENCER).
h = hooks.
go = genital orifice.

The body is covered by a cuticle secreted by the ectodermal cells (hypodermis), beneath which lies a layer of circular muscle-fibres, and beneath these again a layer of longitudinal muscles. The cœlom is ample and is traversed by dorso-ventral muscle-bands, which divide it into a central compartment containing the various organs, suspended by mesenteries, and two lateral ones. There is no heart or circulatory apparatus, and tracheæ or other respiratory organs are also wanting.

The digestive tract is a straight tube extending through the body from the mouth to the terminal anus, giving off no lateral diverticula throughout its course. The nervous system (Fig. 212, *ng*) consists of a ganglionic mass lying below the œsophagus, a comparatively small commissural ring passing round that portion of the digestive tract, without, however, possessing any ganglionic enlargement which can be termed a cerebrum. Various nerves are given off from the mass, two of which extend backwards throughout nearly the entire length of the body. The only sense-organs present are a number of small papillæ on the anterior portion of the body, which are probably tactile in function.

Glandular organs are highly developed. Scattered over the surface of the body are numerous flask-shaped glands, apparently ectodermal in origin, while lying in the cœlom on each side of the mid-gut and extending back almost to the posterior end of the body are two long cæcal tubes, a glandular structure being also connected with them anteriorly. These glands open in the vicinity of the hooks and have hence been termed the hook-glands (Fig. 211, *hg*), and it has been suggested that they secrete a fluid which serves to keep the blood which the parasite ingests from coagulating, being thus similar to the glands in the pharynx of the Leeches which serve the same purpose. Unless the ectodermal glands are excretory, no special organs for the carrying on of that function occur.

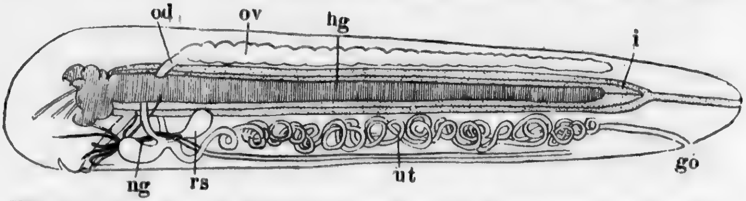

FIG. 212.—DIAGRAM OF STRUCTURE OF FEMALE *Pentastomum* (after SPENCER).

go = genital orifice.
hg = hook-gland.
i = intestine.
ng = nerve-ganglion.
od = oviduct.
ov = ovary.
rs = seminal receptacle.
ut = uterus.

The Pentastomidæ are bisexual, the male being smaller than the female, and recognizable by the situation of the genital orifice (Fig. 211, *go*), which is near the anterior end of the body, while in the female it is near the posterior end. The ovary and testis are both unpaired organs situated beneath the dorsal surface of the body and extending almost its entire length. Anteriorly a pair of oviducts (Fig. 212, *od*) arise from the extremity of the ovary (*ov*) and pass downwards and forwards towards the ventral surface, on nearing which they unite to form a long coiled tube, the uterus (*ut*), which passes backwards to the genital orifice, and just where the two ducts unite they have opening into them a pair of pyriform seminal receptacles (*rs*). The vasa deferentia are also paired, and arise at the anterior end of the testis, passing ventrally towards the genital pore, uniting before they reach it and dilating to form a complicated intromittent organ, from which two tubes with muscular walls and containing spermatozoa project backwards and serve as ejaculatory ducts for the expulsion of the spermatozoa through the intromittent organ.

The only genus belonging to the order is *Pentastomum.*

Development of the Pentastomidæ.—During the life-history of a *Pentastomum* it passes through a marked metamorphosis associated with a change of hosts, recalling what occurs in the *Cestoda.* The ova are passed to the exterior with the excreta of the host, or, in the case of the dog, with the mucous discharge from the nasal passages, and the embryo which hatches out is a decidedly Mitelike form, possessing, however, only two pairs of legs terminating in ungues. No other appendages are present, but the embryo is provided anteriorly with a boring apparatus. If this larva of *P. tænioides*, the parasite of the dog, succeeds in gaining entrance to the digestive tract of a rabbit or cat, for instance, it bores through the wall of the intestine and, reaching the liver, encysts itself. Within the cyst it undergoes several moults, finally assuming a condition similar to the adult except that each annulus bears a circle of hooks. Leaving the cyst, then, it wanders through the tissues of the host, and if while it is in this condition the host is eaten by a dog, it adheres to the mucous membrane of the mouth of the latter, and makes its way into the nasal passages, there moulting again, losing the ring of hooks and assuming the adult form.

The principal reason for supposing *Pentastomum* to be related to the Arachnids is the occurrence of the four-legged larva, which resembles, so far as its external form is concerned, a Mite. The internal structure is very different, however, although certain Arachnid features are indicated; but it is evident that these forms must have undergone an enormous departure from the ancestral form during which the remarkable life-history and peculiar structure have been acquired. The parasitic habits of many Mites, and the general similarity of the body form of *Demodex* to that of *Pentastomum*, suggest the Mites as the ancestors of the latter, a theory which is as plausible as any other which can at present be suggested.

Order **Pycnogonida.**

The Pycnogonida are exclusively marine in habitat, and vary considerably in size, the smaller forms, such as *Tanysty-*

lum, being only about a millimetre in breadth, while the purple *Phoxichilidium* measures over three millimetres from tip to tip of the legs, and the deep-sea form *Collossendeis* has a span of over sixty centimetres. The body proper is comparatively small, the four pairs of long legs which arise from the thorax being exceedingly conspicuous, a feature which has suggested the term *Pantopoda* sometimes applied to the group. Anteriorly there is a well-marked proboscis carrying the mouth at its anterior end, and at the base of this there arise the cheliceræ, which are rather short chelate limbs. The next segment of the body succeeding that which bears the cheliceræ bears upon its dorsal surface the eyes, and may be regarded as a fusion of three segments since it bears three pairs of appendages. The most anterior of these are slender

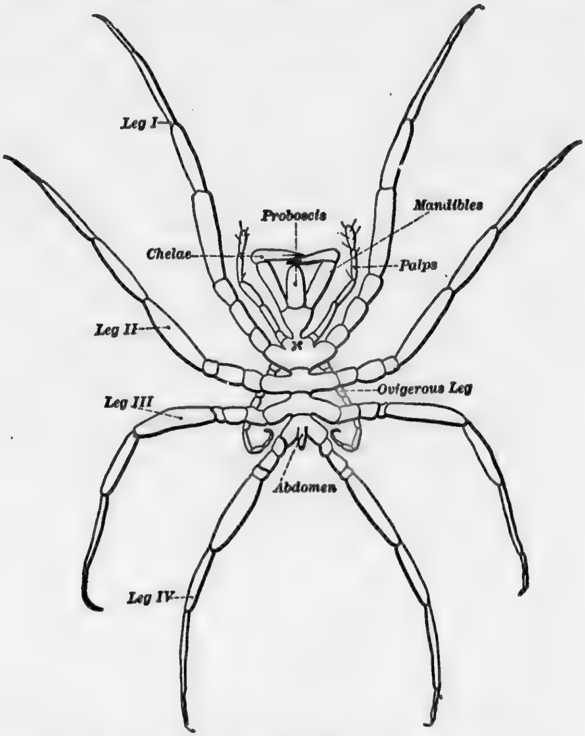

Fig. 213.—*Phoxichilidium maxillare* (after Morgan).

jointed palps; the second pair, wanting in the females of some species, but always present in the males, arise from the ventral surface of the segment, and are curved jointed structures serving to carry the ova; while the third pair are exceeding long jointed walking-legs. The next three segments also bear long walking-legs, the last one having attached to it the usually unsegmented rudimentary abdomen.

The body and the appendages are encased in a well-developed chitinous cuticle, and there are no indications of special respiratory organs. The heart lies immediately beneath the dorsal integument and is a simple tubular organ with from two to three pairs of ostia.

The portion of the digestive tract which lies within the proboscis is lined with chitin and opens behind into an elongated mid-gut, from which long diverticula extend out into the cheliceræ and the proboscis and into the walking-legs, sometimes reaching even into the terminal joints of the latter. A short hind-gut leads to the anus at the tip of the abdomen.

The nervous system consists of a supraœsophageal ganglionic mass, from which arise the optic nerves and those for the cheliceræ, as well as certain nerves passing to the proboscis. Connected with this brain by circumœsophageal commissures is a ventral chain consisting of five pairs of ganglia, the first pair of which is really formed by the fusion of two pairs, distinct in the embryo, and innervates the palps and the ovigerous legs, while the four pairs of walking-legs are supplied by the remaining four pairs. Finally one or two small ganglia also occur, innervating the abdomen. The eyes are four in number, situated at equal intervals upon a small domelike elevation on the dorsum of the first thoracic segment, which, it is to be remembered, is compound. Each eye is covered by cuticle, sometimes thickened so as to form a lens, below which is a layer of cells forming the corneal or cuticular hypodermis. Below this comes a thick layer composed of retinal elements with nuclei in their outer portions and rodlike bodies towards the inner ends where they rest upon a layer of pigment.

These eyes recall the postbacillar eyes of the Arachnids by their structure, but show one remarkable peculiarity, i.e., a distinctly bilateral arrangement both of the corneal hypodermis and of the retinal elements, a distinct raphe being observable upon the inner surface of the eye, the retinal elements being arranged on either side of it. Such a condition as this cannot readily be explained by a simple unilateral inversion such as was described as probably occurring in Arachnidan eyes; it suggests rather an inversion of two sides of a primitive optic cup, the posterior wall at the same time forming the pigmented layer of the eye. Whether the Arachnid eye is not also traceable to such an arrangement, all traces of the original raphe being lost, is a question, though at present it seems more probable that it has been produced by a suppression of the inversion of one side of the cup.

Glands, occurring in the palps and ovigerous legs, have been regarded as excretory in function, but no Malpighian tubules or coxal glands seem to exist, though an homology of the excretory glands just mentioned and of glands occurring in the walking-legs of the males with the latter is not impossible. The Pycnogonids are bisexual, the reproductive organs lying in the thorax and sending out branches into the walking-legs, on the fourth joints of one or more of which they open. As already stated, the male carries the eggs upon his ovigerous legs, fastening them as they are extruded by the female by means of the excretion of the glands occurring upon the walking-legs.

Development and Affinities of the Pycnogonida.—The young Pycnogonid leaves the egg as a six-limbed embryo, which recalls, in a general way, the nauplius of the Crustacea, and indeed has suggested a derivation of the Pycnogonids from that group. The resemblance is, however, but superficial, important differences being found in the structure of the eyes and in the absence of an anus, to say nothing concerning the details of the early development. On the other hand these last, as well as the structure of the eyes, recall the Arachnids, and it seems most probable that the Pycnogonids are to be regarded as having descended from ancestors which might have been included in the type Arachnida.

Order **Tardigrada.**

The Tardigrada are small forms not exceeding a millimetre in length, with an unsegmented body provided with four pairs of short conical appendages tipped with claws, the last pair being situated at the posterior extremity of the body. The body is covered by a cuticle secreted by the subjacent hypodermis, below which and traversing the cœlom is a well-developed system of muscle-bands. There are no special organs either for respiration or circulation.

The mouth (Fig. 214, *m*), surrounded by papillæ, lies at the anterior extremity of the body, and leads into a tubular mouth-cavity containing, imbedded in its walls, a pair of chitinous or partly calcareous teeth, and receiving the ducts of two glands (*sg*) which have been regarded as salivary or perhaps poisonous in function. Behind, this cavity opens into a muscular pharynx which is connected by a short œsophagus with the mid-gut (*s*). At the junction of this with the rectum or hind-gut is a pair of cæcal diverticula (*mg*), possibly Malpighian tubules, and into the hind-gut there also open the ducts of the reproductive organs, the hind-gut thus serving as a cloaca. It opens on the ventral surface of the body a short distance from the posterior extremity and therefore in front of the last pair of appendages.

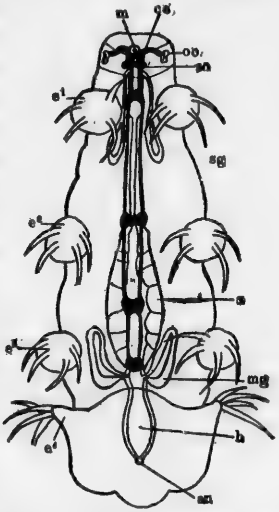

FIG. 214. — DIAGRAM OF STRUCTURE OF *Macrobiotus megalonyx* (after VON ERLANGER).

an = anus.
ce = cerebral ganglion.
$e^1 - e^4$ = appendages.
h = hindgut.
m = mouth.
mg = mid-gut diverticula.
oc = eye.
s = midgut.
sg = salivary (?) glands.
so = subœsophageal ganglia.

The nervous system consists of a supraœsophageal ganglion (*ce*) united with a chain of four pairs of ventral ganglia. No special sense-organs occur except two eyes situated at the sides of the head. The sexes are distinct, the reproductive organ being unpaired and opening into the cloaca, into which opens also in both sexes an unpaired accessory gland.

The Tardigrada occur in water usually, especially in such locations as the gutters on the roofs of houses, though sometimes found also among moss. The group contains but a small number of genera, of which *Macrobiotus* is perhaps the most common.

Affinities of the Tardigrada.—The presence of four pairs of limbs has usually been regarded as pointing to a relationship of these forms with the Acarina, but the absence of all mouth-appendages, the structure of the legs, and the position of the last pair with regard to the anal opening, not to mention the peculiarities of the internal organization, are opposed to any close relationship with the Arachnida. The Tardigrada must be considered as holding an independent position, without distinct indications of relationship with any of the types, until further information as to their primitive relationships has been secured. In addition the embryological history, which has recently been worked out, furnishes no evidence in favor of Arachnidan affinities, and it seems quite probable that the Tardigrades should be removed entirely from among the Arachnida and possibly associated with such forms as the Echinodera.

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CHAPTER XV.

TYPE TRACHEATA.

THE Tracheata are, like the Arachnida, essentially terrestrial forms, for, though a few Insects have adapted themselves to an aquatic mode of life, they are nevertheless air-breathers, living either at the surface of the water or coming to the surface from time to time to renew the air contained in the tracheæ which ramify through the body and serve as respiratory organs. However, a few Insect-larvæ have acquired the power of extracting oxygen from the water by branchia-like processes of the body, but, even in these cases, tracheæ form the organs by which the respiration is carried on, the branchiæ being richly supplied with them.

The body is distinctly segmented (except in *Peripatus*,) and is covered by a chitinous cuticle secreted by the ectodermal cells, which constitute the so-called hypodermis. The appendages are usually uniramous, and with few exceptions (*Peripatus*) are jointed. The anterior pair in all cases are more or less elongated multiarticulate structures provided with sense-hairs, and are situated præorally, while of the remaining pairs, varying in number in different groups, the most anterior pair is specialized to serve as mandibles, while the succeeding one or two pairs usually form maxillæ. Numerous glands of varying function are developed in the hypodermis, the most interesting of which are the crural glands, well developed in *Peripatus*, and represented more or less perfectly in certain other forms. In addition to these, glands which secrete an acrid or offensive fluid (*repugnatorial glands*) are frequently present, as well as others which secrete waxy substances, or even in some cases silk.

The cœlom except in *Peripatus* is lacunar throughout, possessing no definite walls, and is traversed in various directions by muscles, serving to flex or extend the body and to move the appendages. A marked difference between the Tracheata and the Arachnida is the universal absence of an endosternite, a structure of considerable phylogenetic significance in the latter group. A heart is invariably present, lying above the intestine, and situated in a pericardial sinus incompletely partitioned off. In the majority of forms the partition is composed of a varying number of triangular muscles, the alar muscles, which are attached by their bases to the walls of the heart, and by their apices to the body-wall. While at rest they are somewhat vaulted, the convexity being dorsal, and on contraction flatten down, thus enlarging the sinus and causing a flow of blood into it. The heart (Fig. 227, *h*) is elongated and imperfectly divided into a series of chambers, separated by pairs of valves which allow the blood to flow from behind forwards but not in the reverse direction, the heart being closed behind. Ostia are present in the lateral walls to allow of the entrance of blood into the heart-chambers, whence it is propelled through very short arteries which open widely into the lacunar spaces of the cœlom. In many forms a ventral sinus surrounds the ventral ganglionic nerve-chain, the blood flowing in it from before backwards, but with this exception definite vessels are wanting. This is compensated for by the rich branching of the tracheæ, which, as stated, serve as respiratory organs and convey air to all parts of the body; the air is in fact brought directly to the tissues, instead of being carried to them by the blood from limited portions of the surface of the body. The blood is usually colorless, but in some cases is of a bright yellow or green color, owing to pigment contained in the plasma, and it contains in all cases colorless amœboid corpuscles.

The tracheæ (Fig. 215, *tr*) communicate with the exterior along the sides of the body by a varying number of pairs of stigmata (*st*), and may either consist of bunches of unbranched tubes connected with each stigma, or of a number of richly-branching tubes, each one arising from a separate stigma and anastomosing in some cases through some of its branches with the tubes from other stigmata. Each stigma is usually provided with an apparatus by which it may be closed, and in the Insects the air is expired from the tracheæ by the contraction of certain dorso-ventral muscles of the abdomen, which cause a compression of the organs in that region of the body, inspiration following on their relaxation and the consequent re-expansion of the abdomen. In structure the tracheæ are simply to be regarded as invaginations of the body-wall, and consist of a single layer of cells continuous with the hypodermis of the body, lined within—that is to say, on the surface with which the air is in contact—with chitin, which is thickened in such a way as to form a spiral band extending along the tube and serving as a spring to keep its walls apart.

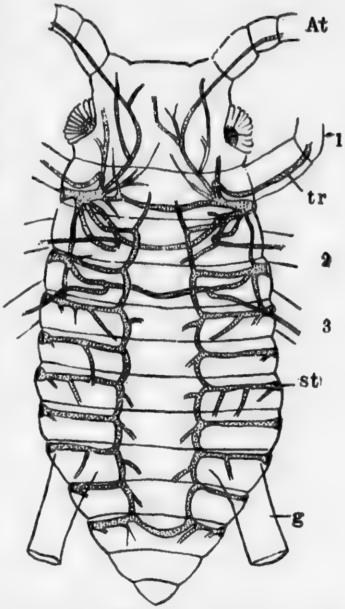

FIG. 215.—FIGURE SHOWING THE DISTRIBUTION OF TRACHEÆ IN *Aphis pelargonii* (after WITLACZIL).

At = antennæ.
g = gland-duct.
st = stigma.
tr = trachea.
1, 2, 3 = thoracic appendages.

The digestive tract is in most groups a straight tube, but in Insects (Fig. 227) it may be coiled in a more or less complex manner and differentiated into several parts. Glands of various kinds are usually associated with it, salivary glands (Fig. 227, *sg*) opening into the anterior portion and Malpighian tubules (*mv*), in connection with the posterior portion, being the most constant in occurrence. It is to be noted that the fore-gut and hind-gut are ectodermal in origin, and that the Malpighian bodies arising as outgrowths from the hind-gut are also ectodermal, differing thus in origin from the similarly-named organs of the Arachnida, which are apparently of endodermal origin, arising from the mid-gut. In function both organs are similar, the Malpighian bodies of Tracheates being excretory.

The nervous system in the less-differentiated members of the type consists of a supracœsophageal ganglionic mass, connected by circumœsophageal commissures with a chain of ventral ganglia, a pair of ganglia corresponding typically with each segment. In the Insecta (Fig. 228) more especially, however, considerable concentration occurs, a number of the postoral ganglia, or, in some cases, all of them, fusing to a single mass. A well-developed stomatogastric or sympathetic nervous system occurs in all forms, arising from the supraœsophageal ganglionic mass by two trunks, which unite to form a single nerve, passing to the digestive tract, and in some cases provided with ganglionic enlargements both paired and unpaired.

Sense-organs of various kinds are well developed in the Tracheata, with the exception of *Peripatus*, in which the only definite organs of special sense are the eyes. In other forms the antennæ and other portions of the body are provided with hairs connected with nerves and serving as tactile organs, and setæ situated upon the mouth-parts and associated with peculiar nerve-endings have been supposed to represent organs of taste, and others again, on the antennæ, olfactory organs. Eyes are very generally present. In *Peripatus* and most Myriapoda simple eyes or ocelli are alone present; in *Peripatus* they resemble closely in structure the eyes of the Annelids or Mollusca (e.g. *Haliotis*, see Fig. 134), but in the Myriapods and Insects they are usually more complicated. Thus in a young larva of *Acilius* (Fig. 216, *A*), a water-beetle, the chitin is thickened to form a cornea (*l*) which lies over a depression of the hypodermis, the cells at the bottom of which are modified to form a retina, each being continuous at its inner end with the optic nerve (*n*), while at its outer end it bears a layer of chitin (*r*). The cells of the lip of the depression have converged together so as to meet beneath the cornea, which is indeed formed by these cells, and a cavity is thus enclosed into which there protrude from among the retinal cells large cells (*mgc*) with chitin deposited on their adjacent surfaces. In a later stage (Fig. 216, *B*) the lips of the depression have united, a continuous corneal hypodermis (*vb*) being thus produced; pigment has been deposited in the lateral cells, and the retinal cells, pigmented near their outer ends and in continuation with the optic nerve, have developed distinct rods (*r*) at their outer ends.

In the Insecta and occasionally in the Myriapoda (*Scutigera*) there are in addition to these simple ocelli compound eyes, situated at the sides of the head and similar in structure to the compound eyes of the Crustacea. Each of the ommatidia of which the eye is composed, and there may be several thousand of them in each eye, consists of an external cornea (Fig. 217, *co*), usually more or less hexagonal in outline, giving the eye a faceted appearance. Beneath the cornea are two cells which secrete it and form the corneal hypodermis, and below these again come four cells, the crystalline-cone cells, which may (*euconous* eyes) or may not (*aconous* eyes) manufacture a crystalline cone (*c*), and finally beneath these is a circle of seven retinular cells (four in *Lepisma*), each one of which is pigmented and manufactures a portion of the chitinlike rhabdom (*rh*) which they surround; these cells are probably continuous at their inner ends with the optic nerve. Additional pigment-cells (*pg*) separate the

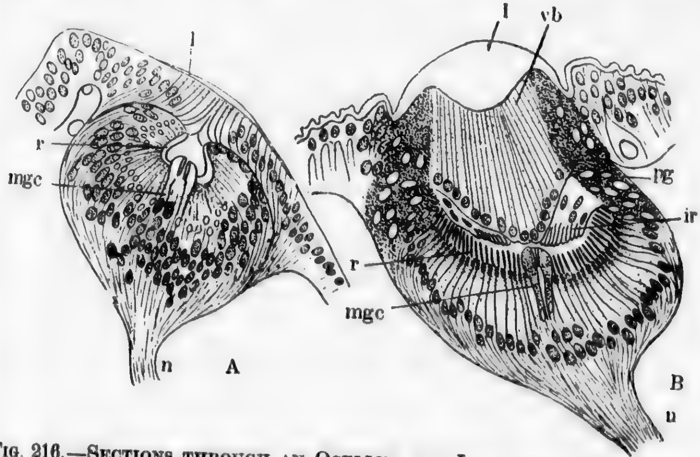

Fig. 216.—Sections through an Ocellus of a Larva of *Acilius* in (*A*) a Very Young and in (*B*) an Older Specimen (after Patten).

ir = inverted rods.
l = cornea.
mgc = median giant cells.
n = nerve.
pg = pigment.
r = rods.
vb = vitreous body.

various ommatidia. Other sense-organs occur in the various groups, but may more satisfactorily be considered in the special descriptions of these groups.

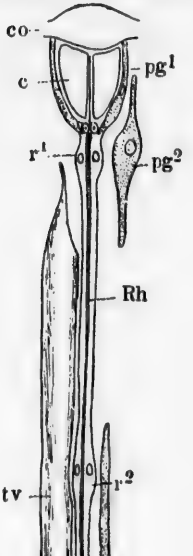

FIG. 217. — OMMATIDIUM OF EYE OF *Musca* (after HICKSON).

c = crystalline cone.
co = cornea.
pg = pigment-cells.
r = retinula-cells.
Rh = rhabdom.
T = trachea.
tv = tracheal dilatation.

True nephridia similar to those of the Annelids occur in *Peripatus*, but in the Myriapods and Insects they are entirely wanting, their place as excretory organs being taken by the Malpighian tubules. The Tracheata are bisexual, the reproductive organs being typically paired and opening to the exterior by ducts, which may unite before reaching the genital orifice. Accessory structures, such as a bursa copulatrix for the reception of the penis and a receptaculum seminis occur in the female, and vesiculæ seminales and accessory glands in the male. The region of the body-wall in the vicinity of the reproductive orifice is in the Insects frequently invaginated, adding a still greater complication, and furthermore the terminal portion of the duct in the male is frequently capable of being evaginated and thus serving as a penis, while integumentary elevations or processes of the last abdominal segment form ovipositors in the females.

I. CLASS **Protracheata.**

This interesting group contains but a single genus, *Peripatus*, which has, however, a wide distribution, species being found in the West Indies and South America, at the Cape of Good Hope and in New Zealand, thus indicating an original wide distribution of the genus which has become extinct except in these few widely-separated regions.

Peripatus is an elongated cylindrical form, measuring in the Cape species (Fig. 218) from about five to six and a half centimetres in length, and is found beneath stones or bark or amongst decaying wood. The body-wall is finely annulated, the annuli not, however, corresponding to segments, and the cuticle is thin, small papillæ being scattered all over the surface of the body, each terminating in a short bristle. The head is but poorly marked off from the rest of the body and bears a pair of many-jointed antennæ, at the base of each of which towards the sides of the head is situated an eye. The mouth lies in the middle of the ventral side of the head and is surrounded by numerous papillæ, and within its cavity is situated a pair of jaws furnished with strong chitinous sickle-shaped teeth. These jaws really represent the second pair of appendages, the third pair being represented by two short papillæ lying at the sides of the head and having at their tips the openings of a pair of glands which extend far back into the body-cavity and from which, when the animal is irritated, there is violently emitted a sticky fluid, whence the glands have been termed the slime-glands (Fig. 219, *sd*). There is no division of the trunk into thoracic and abdominal regions, and it bears a number, varying according to the species from seven to twenty-one pairs, of ambulatory appendages, each of which consists of a proximal stouter and somewhat conical portion bearing rings of papillæ and a more slender short distal portion which bears at its tip a pair of claws (*ungues*). These limbs are unsegmented, differing in this respect from those of the Myriapods and Insects, and are also soft owing to the thinness of the cuticle, a feature which has suggested the name *Malacopoda* formerly applied to the type, as the presence of the terminal ungues has suggested the term *Onychophora*. The anus is situated at the posterior extremity of the body and has on either side of it the anal papillæ which represent the last pair of limbs.

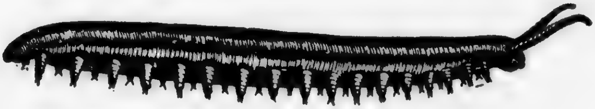

FIG. 218.—*Peripatus capensis* (after MOSELEY from BALFOUR).

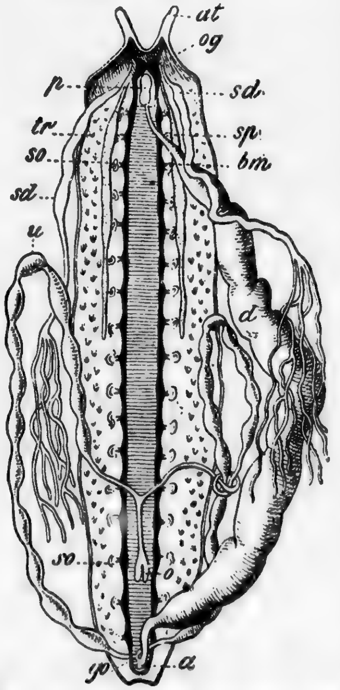

Fig. 219. — Figure showing the Structure of a Female *Peripatus* (from Hertwig).

a = anus.
at = antennæ.
bm = ventral nerve-cord.
d = intestine.
go = opening of reproductive organ.
o = ovary.
og = brain.
p = pharynx.
sd = slime-glands.
so = nephridia.
sp = salivary glands.
tr = tracheæ.
u = uterus.

Beneath the thin cuticle is situated the hypodermis, and beneath this a well-developed dermal muscular system recalling that of the Annelida, being composed of an outer layer of circular muscles, below which are diagonal fibres, and below these again strongly-developed longitudinal muscles arranged in bundles, two of which are situated dorsally, two laterally, and three ventrally. In addition to these, dorso-ventral bands occur passing across the cœlom and dividing it into three chambers, one median and two lateral, and special muscles are also present for moving the limbs.

The cœlom is tolerably capacious and consists of two portions. The larger portion is divided by partitions into several subordinate cavities (Fig. 220), and is lined throughout by a peritoneal epithelium which covers the various organs. From it are, however, separated certain cavities with definite walls, which stand in relation to the nephridia and the reproductive organs and will be spoken of in connection with these organs. A heart (Fig. 220, *h*) of a tubular form extends throughout almost the entire length of the body, lying in a pericardial space (Fig. 220, *pc*) incompletely separated from the rest of the cœlom by a fenestrated transverse partition. A pair of ostia are situated on the dorsal surface of the heart in each metamere, and pass the blood into the heart from the pericardial space. Respiration is performed by tracheæ (Fig. 219, *tr*) consisting of slender unbranched tubes which arise in bunches from stigmata, either scattered irregularly over the surface of the body in considerable numbers or else arranged, as in *P. capensis*, somewhat imperfectly in two rows upon the dorsal and two on the ventral surface of the body.

The mouth opens into the mouth-cavity containing the mandibles, and this communicates posteriorly with a muscular pharynx, and has opening into it the ducts of two long tubular salivary glands (*sp*) which extend through more than half the length of the body. The pharynx (*p*) communicates by a short œsophagus with the stomach, which extends as a straight tube almost to the extremity of the body, where a short rectum places it in connection with the anus. The pharynx and œsophagus and the rectum are lined with chitin and represent the fore-gut and hind-gut of other Tracheates, the stomach being the mid-gut. No Malpighian tubules or other diverticula of the intestine occur.

The nervous system shows several highly-interesting features. There is, as is usual in metameric animals, a supra-œsophageal ganglion-mass (Fig. 219, *og*) composed of at least two and probably three pairs of ganglia, of which the first supplies the antennæ and the second the mandibles, while a third pair lies at the sides in close contact with the second pair and sends nerves to the oral papillæ. These latter are, however, postoral and ventral in position, and from them there extend back two ventral cords (*bm*) which in each metamere dilate into a ganglionic swelling. The two ventral cords are, however, widely separated, lying in the lateral chambers of the cœlom (Fig. 220), and are connected by a large number of cross-commissures—a condition which recalls the arrangement in the Amphineurous Mollusca (see Fig. 124), the similarity being further increased by the facts that the two cords unite behind and above the rectum, as in the Solenogastres, and that the ganglion-cells are not confined to the enlargements but are scattered all along the cords. The eyes are the only special organs of sense; their structure has been already indicated (p. 472).

One of the most interesting features of *Peripatus* is the occurrence in it of typical nephridia (Fig. 219, *so*). Upon the under surface of the proximal portion of each limb, with the exception of the penultimate or last pair, there is a slitlike opening which leads into a more or less coiled tube lying in the cœlomic compartment, which extends into the limb and terminates in a thin-walled vesicle. These tubes are nephridia, the terminal vesicles (Fig. 220, *ne*) representing portions of the cœlom into which the nephridia open—a fact indicated by their embryological history. The nephridia are thus exactly comparable in every respect with the nephridia of Annelids, communicating at one extremity with the exterior, and at the other with the cœlomic cavity. It is interesting to note that the development of the salivary glands shows that

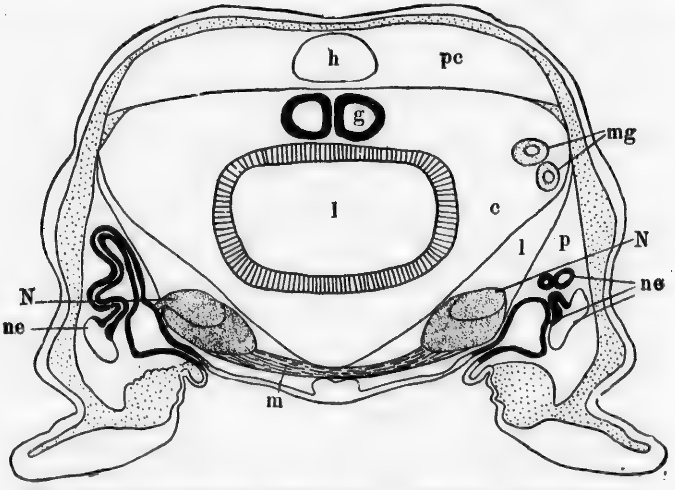

FIG. 220.—TRANSVERSE SECTION OF A *Peripatus* (after SEDGWICK).

c = central compartment of cœlom.
g = reproductive organ.
h = heart.
I = intestine.
l = lateral compartment of cœlom.
m = muscles.
mg = slime-glands.
N = ventral nerve-cords.
ne = nephridia.
p = compartment of cœlom which extends into the limb.
pc = pericardial compartment of the cœlom.

they are the modified nephridia of the third segment of the body, that which bears the oral papillæ, and furthermore it is to be noted that in the last or next to last (according to the species) limb-bearing segment, in which nephridia are wanting, are found the ducts of the reproductive organs—a fact which suggests that these are also modified nephridia. This idea is confirmed by the development of the genital ducts, and carries with it the corollary that the cavities of the reproductive organs (Fig. 220, *g*) are portions of the cœlom, just as they were shown to be in the Mollusca (see p. 288).

In addition to the nephridia there are associated with certain of the appendages glands which open on the under surface of their basal moiety and are termed the crural glands. In *P. capensis* they are present in all the appendages except the more anterior one, and the slime-glands are simply the highly-modified crural glands of the oral papillæ, those of the last pair of appendages in the males of this species being similarly elongated though possessing a different function. In *P. Edwardsii*, however, crural glands occur only in the males, and in these only in a few segments immediately in front of that bearing the reproductive opening.

The Protracheata are bisexual, the female usually being somewhat larger than the male. The ovaries are paired, though included within a common capsule, and lie in the posterior part of the cœlom. They are continuous with two uteri, which immediately at their origin are united by a transverse tube, and each bears a receptaculum ovorum and a receptaculum seminis. Beyond this each continues its course along the side of the body, passing backwards to finally unite at the common orifice, lying a short distance in front of the anus on the ventral surface of the body. The testes are slender paired structures which are continuous with a slender vas deferens. This dilates a short distance from the testis into a vesicula seminalis and then unites with its fellow of the opposite side to form a slender somewhat coiled tube, the ductus ejaculatorius, in the terminal portion of which the spermatozoa are united together into a spermatophore. The Protracheata are viviparous.

Affinities of the Protracheata.—Peripatus is a highly-suggestive form on account of possessing both Annelidan and Tracheate characteristics, so that it has been generally regarded as indicating a descent of the Tracheate forms from the Annelids. Its Annelidan features are, first, the presence of a distinct dermal muscular system; second, the occurrence of crural glands which seem to be homologues of the glands which secrete the setæ in the Annelida; third, the possession of nephridia corresponding closely to those of the Annelids; and fourth, the structure of the eyes. On the other hand, its Tracheate affinities are shown by the claw-tipped feet, by the adaptation of the feet (mandibles) for masticatory purposes, by the tendency towards a concentration of the anterior segments to form a head, and by the occurrence of tracheæ. Both these sets of features are highly important, and, taken with the wide distribution of *Peripatus*, point strongly to its being the representative of a connecting link between Tracheates and Annelida, a phylogeny which may be considered more in detail at the close of this chapter.

II. CLASS **Myriapoda.**

The Myriapoda possess a distinct head composed of a number of fused segments and followed by a distinctly-segmented body formed of a varying number of segments, all of which are more or less similar, there being no differentiation of a thorax and abdomen. A single pair of appendages as a rule is borne by each segment, with the exception, in some cases, of the last. The most anterior pair are usually long multiarticulate antennæ, the second pair mandibles, and the third and fourth, or the third alone, are modified to form maxillæ; the succeeding pairs, with one or two exceptions, are ambulatory, and are jointed and tipped by a claw.

The chitinous cuticle is generally thick, and consequently no definite system of dermal muscles is developed, a number of separate muscles occurring in each segment for moving the appendages and the various segments upon one another. Glands of various kinds opening upon the surface of the body occur, the most important being glands or protrusible glandular sacs situated upon the basal joints of a number of the appendages and apparently homologous with the crural glands of *Peripatus*.

The heart is in all forms very long, extending through the entire length of the body behind the head, and possessing just as many chambers and pairs of alar muscles as there are trunk-segments. The number of stigmata vary, in some forms only a single pair occurring, while in others there is a pair on each segment of the trunk; and the form of the tracheæ varies also, as they are sometimes branched and sometimes arranged in bunches composed of a number of unbranched tubes.

The digestive tract is almost always a straight tube, extending through the body to the terminal anus. The mouth is guarded in front by a well-developed upper lip or labrum, while the fusion of the maxillæ behind it in many forms produces a lower lip. It leads into an ectodermal fore-gut, and this into an endodermal mid-gut, which is usually provided with a number of unbranched diverticula termed hepatic cæca. One or two pairs of Malpighian tubules open into the anterior end of the ectodermal rectum, and serve as excretory organs.

The nervous system except in the head region shows but little trace of concentration, there being as a rule in each segment of the trunk a pair of ganglia. The antennal ganglia are fused with the supraœsophageal ganglionic mass which sends off branches to the ocelli; these may be quite numerous, though compound eyes do not as a rule occur. A sympathetic system is present as in other Tracheates.

There are no nephridia so far as known in the group, the excretion being performed by the Malpighian tubules. The reproductive organs are paired, and open to the exterior in some cases by paired orifices, but more usually by a single opening, which may be situated either far forwards, or else in other cases near the posterior extremity of the body.

1. Order **Pauropoda.**

The order Pauropoda contains a few small forms in which the trunk possesses twelve metameres and but ten pairs of appendages, which, with the exception of the rudimentary first pair, are six-jointed and terminate in a claw. When viewed from the dorsal surface, the segments appear to be less numerous than the appendages, a condition which results from the fusion of certain metameres in pairs, so that two pairs of appendages appear to belong to some of the segments, the double nature of which is further shown by the occurrence in them of two pairs of nerve-ganglia. The antennæ (Fig. 221) are remarkable in form, consisting of a four-jointed basal portion which bifurcates at the tip, one of the bifurcations bearing two long flagella and a peculiar spherical stalked body, while the other one bears a single flagellum. Mandibles are present, and there is also a single pair of but poorly-developed maxillæ.

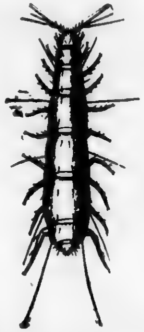
Fig. 221. — *Pauropus Huxleyi* (from Leunis).

Tracheæ or other respiratory organs are not yet known to exist, nor have any indications of a circulatory system been discovered up to the present. The reproductive opening is situated upon the second trunk-segment.

None of the members of the order exceed a little over a millimeter in length. The genus *Pauropus* is characterized by the body being elongated and cylindrical, and by its active movements, while in *Eurypauropus* the body is flattened and relatively broad, and the movements are sluggish.

2. Order **Diplopoda**.

The Diplopoda, sometimes termed the Chilognatha, are popularly known as the Millipedes on account of the commoner forms possessing an unusually large number of appendages. The body is usually cylindrical and provided with a hard cuticle, and many forms are in the habit of rolling themselves when disturbed into a ball or a helixlike coil, thus protecting the more delicate ventral surface of the body. The antennæ (Fig. 222, *at*) are generally seven-jointed and are never very long, and the mandibles are strong jaws without palps. In front of the mouth is a well-developed upper lip (*ul*), while behind it is a lower lip formed by a fusion of the maxillæ (*mx*). According to some authors this lower lip represents two pairs of appendages, but its innervation and embryological history seem to be opposed to this view. The segments behind the head vary in number in different genera from eleven (*Glomeris*) to over one hundred, and the number of appendages is much greater still, since the majority of the segments bear two pairs of limbs and in reality represent each two metameres. The four or five anterior trunk-segments are, however, single, bearing but a single pair of limbs (Fig. 222), and one of them—in some cases the first, in others the second, but more usually the third (*Iulus*)—is entirely destitute of appendages. The last few segments also carry but a single pair of appendages, as does also the seventh segment in the males, the appendages of which are usually modified to serve as copulatory organs.

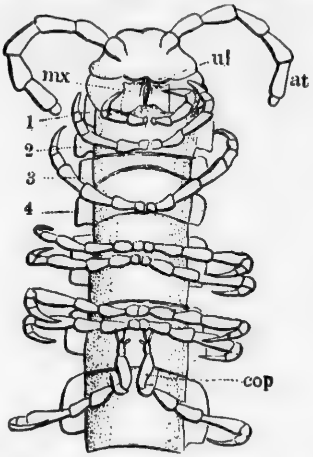

Fig. 222.—Anterior Portion of a Diplopod.

at = antenna.
cop = copulatory appendages.
mx = maxilla.
ul = upper lip.
1, 2, 3, 4 = the four anterior trunk-segments.

Stigmata occur on each of the trunk-segments, the double segments bearing two pairs, situated on the ventral surface near the coxal joints of the limbs. Each one has in connection with it a bunch of unbranched tracheæ, a condition recalling somewhat that of *Peripatus*, although the location of the stigmata is much more regular and definite. Upon the dorsal surface of the body there is in most species a row of pores which have been mistaken for stigmata, but are really the openings of glands (*gl. repugnatoria*) secreting an oily evil-smelling fluid which serves as a means of defence. In the genus *Polydesmus* the secretion contains hydrocyanic acid. Crural glands do not as a rule occur, but protrusible warts occurring on the coxal joints of a number of legs in some genera (*Lysiopetalum*) have been regarded as homologous structures.

The nervous system has the characteristic Myriapodan arrangement, each of the double segments possessing two pairs of ganglia. Eyes are usually present and are always simple, varying in number from two to as many as eighty.

The Diplopoda are bisexual, and the ovaries or testes form a single mass from which two ducts, or one which later divides into two, arise and pass forward to open on the ventral surface of the body between the second and third trunk-segments. The embryos when first hatched out possess but three pairs of legs, situated upon the first, third, and fourth segments in *Strongylosoma*, and on the first, second, and fourth in *Iulus*, one or more segments without appendages lying behind the fourth pair. By successive moults new segments and appendages are added and the form of the adult gradually acquired.

The Diplopoda live for the most part under stones, etc., or among dead leaves, and find their food in decaying vegetable matter, though some forms will attack living vegetation and may prove thereby injurious to gardens. The commonest form, *Iulus*, may readily be obtained under stones or boards all through the summer.

3. Order **Chilopoda.**

The Chilopoda, or Centipedes, are very different in their habits from the Millipedes, being carnivorous and provided with poison-glands which render the larger forms of *Scolopendra* dangerous even to man. The body is as a rule somewhat flattened and less hard than that of the Diplopoda. The antennæ (Fig. 223, *at*) are usually long, with at least twelve joints, and may be as long as the body, while the mouth-parts are much more complicated than in the Diplopoda. The mandibles and upper lip resemble the corresponding parts in that group, but the maxillæ (*mx*) are jaw-like, are not fused together, and in some forms (*Geophilus*) bear a palp. Behind the maxillæ comes a pair of second maxillæ (mx^2), which, however, do not serve as jaws but are reduced to a pair of palplike structures, and behind these again is a pair of maxillipeds (*mxp*), the appendages of the first trunk-segment, with their basal joints fused to form a lower lip supporting a four-jointed palp, the last joint of which is clawlike and is perforated by the duct of a poison-gland. Each trunk-segment, of which there may be over a hundred, bears but a single pair of appendages, there being no compound segments as in the Diplopoda. Each leg is as a rule seven-jointed, the coxal joints of those of the same segment being widely separated, and there is no modification of the seventh pair to serve as copulatory organs, though the pair of the penultimate segment are much reduced in size and lie at the sides of the reproductive orifice.

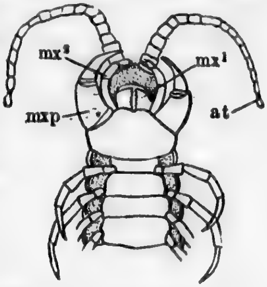

FIG. 223.—ANTERIOR PORTION OF A CHILOPOD.
at = antennæ.
*mx*¹ = maxilla.
*mx*² = second maxilla.
mxp = maxilliped.

Stigmata are usually wanting in the first three trunk-segments, but occur in a certain number of the others, lying usually laterally between the segments except in *Scutigera*, in which they have a dorsal position. They open into branched tracheal trunks which usually anastomose with one another, though in *Scutigera* they open into sacs from which a large number of simple unbranched tracheal tubes arise arranged in a bunch as in the Diplopoda. Crural glands occur on the coxal joints of several of the posterior appendages.

The nervous system is arranged as in other Myriapods, and simple eyes are usually present, in *Scutigera* only being closely aggregated together to form a faceted eye. This, however, is not a compound eye exactly similar to that of the Insects, but is to be regarded simply as a close aggregation of simple eyes.

The reproductive organs are usually paired, and the sexes separate. The ducts unite before opening to the exterior, so that there is but a single opening situated on the antepenultimate segment of the trunk, the appendages of which are greatly reduced in size. The embryos of *Scolopendra* and *Geophilus* leave the egg with almost the same number of appendages as the adult, while those of *Scutigera* and *Lithobius* possess but seven pairs of legs (in addition to the maxillipeds) and gradually acquire others by successive moults.

In *Scutigera*, a form which frequents the warmer parts of the world, the dorsal surface of the body is covered in by eight shieldlike folds which conceal a certain number of the segments, which are about fifteen in number. *Lithobius* has the same number of segments and is common under stones, etc., as is also *Geophilus* and *Scolopendra*, both elongated forms, the former usually without eyes, while the latter usually possesses them but has only some nine or ten pairs of stigmata. Some of the species of *Scolopendra*, especially those living in warm countries, grow to a considerable size and are capable of inflicting a dangerous wound.

4. Order **Symphyla.**

The order Symphyla contains a number of small forms referable to one or two genera, of which the best known is the genus *Scolopendrella* (Fig. 224). Unfortunately the details of the structure of the members of the group are by no means well known, a circumstance all the more to be regretted since *Scolopendrella* seems to possess certain Insect-like features. The body is elongated, and on the dorsal surface possesses a number of plates which overlap slightly, but which do not correspond in number with the appendages. The head bears a pair of long many-jointed antennæ, and behind these, in the region of the mouth, is a pair of mandibles and a single pair of maxillæ, both these last-named appendages being deeply imbedded as it were in the tissues of the head, their tips only projecting. The first pair of trunk-appendages is not transformed into maxillipeds as in the Chilopoda, but is ambulatory in function, and most, but not all, of the succeeding segments, of which there are apparently fourteen, bear a pair of five-jointed legs terminated by two claws. Attached to the coxal joints of most of these appendages is a peculiar spurlike process, internal to which is situated a protrusible

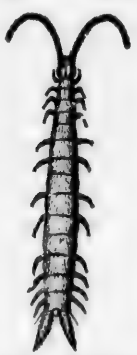

FIG. 224.— *Scolopendrella immaculata* (from LEUNIS).

glandular sac which is probably to be regarded as a crural gland. The last pair of appendages may be unjointed, each bearing a tactile seta, and attached to the last segment is a pair of conical processes each of which has opening at its tip the duct of a spinning-gland.

Two stigmata, situated at the base of the antennæ, are the only ones which occur, their position being very remarkable. They open into bunches of branched tracheæ which extend throughout the greater portion of the body, leaving only the appendages and the posterior part of the trunk destitute of an air-supply. The Malpighian tubules attached to the hind-gut are very long, and salivary glands opening upon the maxillæ are present.

Eyes do not occur. Both the male and female reproductive organs are paired. There is but a single genital pore in either sex, situated in the mid-ventral line towards the front of the fourth trunk-segment, and the oviducts or vasa deferentia unite before communicating with it. Very little is known as yet concerning the development of *Scolopendrella*. It has been considered by some to show marked affinities with the Insecta, and the name given to the order implies the possibility of its being a connecting link between that group and the Myriapoda. The spurlike processes have been regarded as limb-rudiments, in which case it seems possible that each segment may really be a double segment and that the Symphyla have close affinities with the Diplopoda.

III. Class **Insecta.**

The class Insecta is far richer in species than any other class of animals, some two hundred thousand species belonging to it being known to exist, and of these about eighty thousand are beetles. A very large number are provided with organs of flight and may be termed aërial; others are terrestrial, living either upon the surface of the earth or excavating burrows beneath its surface; while some have adapted themselves to an aquatic mode of life, and others are even marine, members of the genus *Halobates* being found on the surface of the ocean many miles from land. Many species, living as they do upon vegetable food either in the adult or larval stages, and occurring occasionally in enormous numbers, form powerful enemies to the horticulturist and agriculturist, the Rocky Mountain Locust, for example, devastating at times the crops, while fruit and forest trees are injured by the attacks of other forms.

The Insecta differ from other Tracheata in having the body divided into three well-marked regions. The most anterior of these is the unsegmented head, bearing the antennæ and the masticatory appendages, and immediately following it is the *thorax*, composed of three segments, the *prothorax*, *mesothorax*, and *metathorax*, each of the last two bearing usually a pair of wings upon its dorsal surface, while posteriorly is the segmented abdomen composed typically of ten segments, sometimes as broad as the thorax at the junction with that region, sometimes contracted to a narrow stalk. In many cases, however, the apparent number of segments falls below ten owing to the fusion of certain of the posterior segments or the union of the anterior segment with the thorax, and in the Butterflies and two-winged Flies the thoracic segments seem to be reduced to two owing to the close association of the metathorax with the first abdominal segment.

Four pairs of appendages are borne by the head. The antennæ, and indeed all the appendages, vary greatly in shape in the various groups, but are usually long slender multiarticulate structures provided with sensory hairs. The masticatory appendages are a pair of mandibles and two pairs of maxillæ, which are variously specialized for biting, piercing, or sucking. The most typical condition is that in which the entire apparatus is adapted for biting and that may be described here, leaving special modifications to be considered in connection with the orders in which they occur. The mandibles (Fig. 225, *C*) are strong unjointed toothed plates which meet together in the middle line and are provided with strong muscles. The first maxillæ, or, as they are usually termed, the maxillæ (Fig. 225, *B*), on the other hand are distinctly jointed, and consist of a basal joint, or *cardo*, succeeded by a second joint, or *stipes*, which bears on its outer side a multiarticulate *palpus* (*p*) and terminates in one or two unsegmented plates of which the innermost is usually toothed. The second maxillæ (Fig. 225, *A*) are also jointed and are fused together to form a lower lip, or *labium*. The fused basal joints form the *submentum* (*sm*), the second joints the *mentum* (*m*), which bears, as does the stipes of the maxillæ, a jointed palp (*p*) and terminates frequently in two unjointed plate-like processes. The three pairs of appendages of the thorax are typically ambulatory, but are modified for clasping, swimming, digging, etc., according to the habits of the insect. They typically consist of a basal joint, the *coxa*, succeeded by one or two small joints, the *trochanter*, upon which follow a *femur*, a *tibia*, and a *tarsus*, the last consisting of five (occasionally four) short joints, the terminal one bearing two claws or ungues. Abdominal appendages are represented only by *cerci*, which are usually many-jointed structures occurring near the posterior end of the body in many groups of Insecta (Fig. 236), and by the pairs of spurlike processes which occur on a number of the abdominal segments of the Thysanura and which recall the spurs on the trunk-segments of *Scolopendrella*. In the embryos of probably all forms rudimentary appendages are found on some of the abdominal segments, but they later disappear, showing, however, a descent of the Insecta from forms in which abdominal appendages were functional in the adult. Processes of various kinds, such as *styli*, ovipositors, and copulatory organs, are frequently borne by the posterior abdominal segments, but these do not seem to be equivalent to appendages.

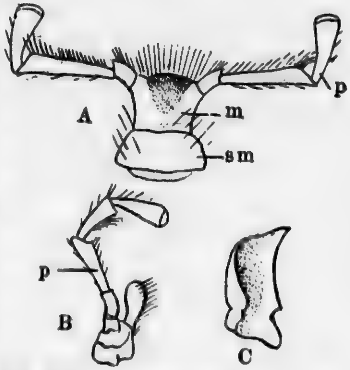

FIG. 225.—MOUTH-PARTS OF A BEETLE, *Monohammus*.
A = labium.
B = maxilla.
C = mandible.

As stated, a pair of wings is usually borne by the meso- and metathoracic segments. These structures are entirely wanting in the lowest insects, the Thysanura and Collembola, as well as in certain forms belonging to other groups which have lost them through parasitism (*Mallophaga, Pulex, Melophagus*) or other causes (Worker and Soldier Termites, Neuter Ants, the females of some Moths). They are, when their possessors are first hatched out, saclike structures, processes of the body-wall, tracheæ enclosed within blood-lacunæ extending from the body into their cavities. Later, however, the walls of the sac come into contact, the cavity being obliterated, the tracheæ with the blood-lacunæ in which they are situated remaining enclosed within the flat plates so formed and constituting the so-called veins of the wing, which have in most species a characteristic and constant arrangement. In certain forms the anterior wings become more or less thickened by the deposition in them of additional chitin, and may form hard plates (*elytra*, Fig. 239) which serve as a cover and protection foı the posterior wings, which in such cases are alone used in flight. In the two-winged Flies (Fig. 244) the posterior wings are very much reduced, being represented only by two small club-shaped structures termed "balancers," attached to the sides of the metathorax.

The body is enclosed in a chitinous cuticle, usually of some firmness and frequently bearing numerous hairlike processes, certain of which serve as sense-organs. Glands opening on the surface of the body also occur in connection with the integument; for example, peculiar protrusible glandular sacs are situated, two or four on each segment, on the abdominal segments of the Thysanura and Collembola close to the spurlike abdominal appendages present in those forms, and are in all probability homologous with the similar structures of *Scolopendrella* and therefore presumably represent crural glands. These glands appear, however, to be wanting in other insects. Many genera of Hemiptera possess glands which produce a malodorous secretion, and wax-glands occur in the Plant-lice (*Coccidæ*) and Bees, the latter also possessing poison-glands in connection with a complicated stinging-apparatus, which is a modified ovipositor.

The respiratory stigmata vary greatly in number in different groups of Insects. In the wingless Thysanura and Collembola there are usually ten stigmata on each side of the body, two being situated on the sides of the thorax and eight on the abdomen, but in *Campodea* the number is reduced to three pairs, which occur upon the thorax. In the winged forms the number also varies somewhat, but there are again typically ten pairs, arranged as in the Thysanura. They lead into short trunks, which, in *Campodea*, ramify through the body without anastomosing, but more usually they are united on each side of the body by a longitudinal tube, from which pass off numerous branches penetrating to all parts of the body, and transverse connecting tubes passing between the systems of the two sides (see Fig. 215). In certain forms which are active flyers the longitudinal tubes are frequently dilated to form air-sacs, as in the Bees, or numerous air-sacs may occur which may be more or less emptied or expanded according to the will of the insect, the specific gravity of the body being thus altered. In the aquatic larvæ which occur in some forms, such as the May-flies (Ephemeridæ, Fig. 226), adaptations occur for the breathing of air dissolved in the water, the sides of the body in the abdominal region being prolonged into a number of pairs of platelike processes, into which branches of the tracheæ project, an interchange of the gases contained in the tracheæ for those dissolved in the water taking place through the walls of the plates, similarly to what occurs in the branchiæ of the Crustacea, though in these forms the exchange is directly with the gases of the blood. These structures are consequently termed tracheal branchiæ, and while they are functional, the stigmata are closed, only opening when the adult stage is reached and a terrestrial life adopted. As a rule the tracheal branchiæ are thrown off at the moult by which the adult form is reached, but in a few forms they persist throughout life.

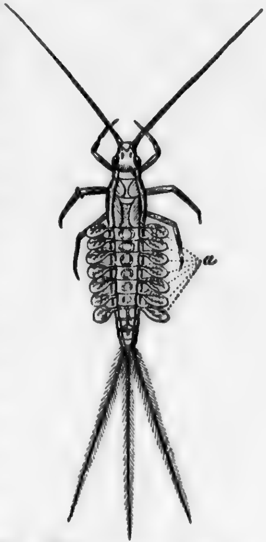

FIG. 226.—LARVA OF AN EPHEMERID (from LEUNIS). *a* = tracheal branchiæ.

A dermal muscular system does not exist, but complicated and well-developed muscles are present for the movement of the various parts of the body, those occurring in the thorax being especially well developed and serving for the movement of the limbs and wings. As in other Tracheates the cœlom is lacunar, and the heart lies in a pericardial sinus below the dorsal surface of the body, alar muscles extending from it to the walls of the body and partly dividing the sinus into a dorsal and a ventral chamber. In the Thysanura the heart extends from the posterior thoracic region throughout the greater part of the abdomen, and consists of nine chambers separated by valves and each provided with a pair of ostia and a pair of alar muscles. In the majority of forms (Fig. 227, *h*), however, the heart is entirely confined to the abdominal region, and the number of chambers, though frequently as high as eight, may be greatly reduced. An aorta extends forwards from the anterior chamber into the head, in the Butterflies (Fig. 227) dilating in the thorax to form a secondary heart (*ah*), and sends off branches which quickly empty into the lacunar spaces.

The greater portion of the abdomen is occupied by a peculiar tissue, termed the fat-body, in which the various organs are more or less imbedded, and which receives its name from the fact that its cells contain globules of fatty matter, and in the adult insect usually also concretions of uric acid. It is not necessarily confined to the abdomen, but may extend into the thorax or even into the head. In certain Beetles—the Fireflies (Lampyridæ) and *Pyrophorus* of the West Indies—certain regions of the body, especially the abdomen, and, in *Pyrophorus*, two spots upon the thorax, give out under certain conditions, apparently under control of the animal, a very bright light, usually spoken of as a phosphorescence. The tissue which produces the light is the fat-body, or special portions of it abundantly supplied by tracheæ, and the process seems to be one of oxidation of phosphorus-containing substances. The exact nature of the phenomenon is but poorly understood at present, and it is not possible by any means at our disposal to produce in the laboratory a light equal in intensity to that of the Firefly with the expenditure of as little energy.

The digestive tract is as a rule much more complicated than in other classes of Tracheates and is generally more or less twisted or contorted in the abdominal region, so that usually it is longer than the body. The mouth is bounded in front by a usually large upper lip or *labrum*, generally described with the mouth-parts, but distinguished from them in not representing a pair of appendages. The anterior portion of the intestine, the fore-gut, is ectodermal in origin as in other Tracheates and consists of a mouth-cavity into which, or in its neighborhood, the ducts of one or more generally well-developed salivary glands (Fig. 227, *sg*) open. The secretion of these glands varies considerably in different forms, one of the pairs present in the larvæ of the Butterflies and certain Moths being transformed into silk-spinning glands, the silk of the Silkworm being a product of their activity. When digestive the secretion seems to have a peptonizing effect as well as the power of transforming starch into sugar, and is consequently of considerable digestive importance. The mouth-cavity opens behind into an

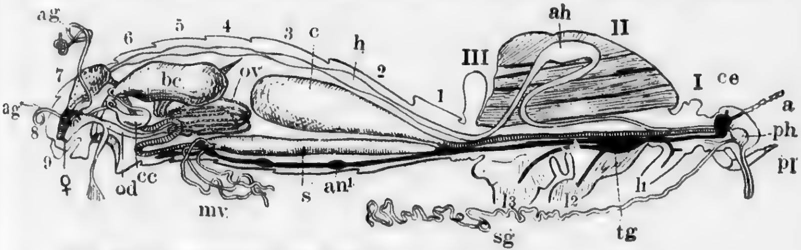

FIG. 227.—STRUCTURE OF BUTTERFLY, *Danais archippus* (after BURGESS).

a = antenna.
ag = accessory gland.
ah = accessory heart.
an = abdominal ganglion.
bc = bursa copulatrix.
c = crop.
cc = canal uniting *bc* and oviduct.
ce = cerebral ganglion.
h = heart.
l = thoracic limbs.

mv = Malpighian tubules.
od = oviduct.
ov = ovary.
ph = pharynx.
pl = palp.
s = stomach.
sg = salivary gland.
tg = thoracic ganglion.
I-III = thoracic segments.
1-9 = abdominal segments.

œsophagus, whose posterior region is frequently dilated into a crop (Fig. 227, *c*) which in some Beetles is lined with chitinous teeth or bars and whose walls are muscular, the apparatus probably serving for a further mastication of the food. The mid-gut which succeeds the crop is usually dilated into a stomach (*s*), lined in some cases by glandular cells, or, in others, having opening into it numerous glandular diverticula, the so-called liver-pouches. The hind-gut, like the fore-gut of ectodermal origin, has opening into its anterior extremity the Malpighian tubules (*mv*), which vary considerably in number, amounting to nearly one hundred in some Hymenopterans, though more usually limited to from four to eight. They are excretory in function, and are apparently the only excretory organs which occur. The anus is situated at the extremity of the body, and in close proximity to it odoriferous glands frequently open into the hind-gut, serving as organs of defence. In some cases they secrete an acrid fluid which, as in the Bombardier beetle (*Brachinus*), can be expelled with almost explosive force.

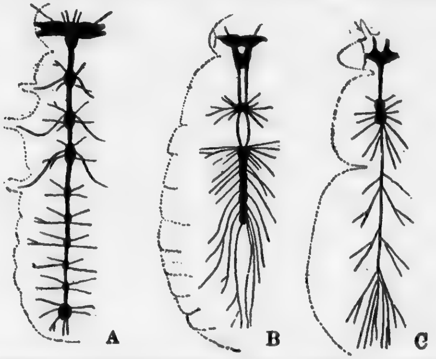

FIG. 228.—DIFFERENT ARRANGEMENTS OF THE NERVOUS SYSTEM IN INSECTS (from GEGENBAUR). *A*, *Termes*; *B*, *Dytiscus*; *C*, a fly.

The nervous system in forms where it shows the least amount of modification (Fig. 228, *A*) consists (1) of a supra-œsophageal mass composed apparently of three pairs of ganglia and supplying the eyes and the antennæ; (2) of a sub-œsophageal mass composed also of three pairs of ganglia supplying the segments indicated by the mandibles, the maxillæ, and the labium; (3) of three pairs of ganglia in the corresponding thoracic segments; and (4) of a chain of abdominal ganglia, a pair occurring in each segment except usually the last two or three, in which a compound ganglion occurs. Frequently, however, this typical condition is modified by a greater or less concentration of the various ganglia, the thoracic ganglia fusing to a single mass, as may also, more or less perfectly, the ganglia of the abdominal chain (Fig. 228, *B*), and the latter may even unite with the thoracic ganglia to form a single mass situated in the thorax, as in certain two-winged flies (Fig. 228, *C*). A visceral system is usually present arising from the supraœsophageal (cerebral) mass and being distributed to the walls of the digestive tract.

The antennæ of insects seem to act as sense-organs, and serve apparently to control the flight, since when removed the insect is not able to fly with its accustomed ability. So too it seems probable that in the Ants and Roaches these appendages are the seat of the olfactory sense, and in the Mosquito it seems that certain hairs upon them may be auditory in function. Compound eyes, frequently consisting of several thousand ommatidia, are usually present, as well as a small number of simple eyes (ocelli) situated upon the dorsal surface of the head. Special organs, which have usually been considered auditory, also occur in many forms, varying considerably in complexity. In its simple form such an organ consists of a single nerve-fibre which dilates into a ganglion-cell prolonged into a terminal hair which is enclosed within a sheath fastened at one end to the wall of the body. This whole apparatus is termed a *chordotonal organ*, and there is usually attached to the sheath just where the hair arises from the ganglion a ligament, which is also inserted into the body-wall. In the majority of cases a number of ganglion-cells and hairs are associated to form a chordotonal organ (Fig. 229), the various hairs sometimes being grouped within a single sheath,—sometimes, however, spreading out in a fanlike manner, each possessing its own sheath. These organs occur in various parts of the body, on the antennæ or on the limbs. In the grasshoppers (Acridiidæ) the first abdominal segment bears on either side a thin tense membrane, a thinned portion of the cuticle, recalling the tympanic membrane of the human ear, beneath and in connection with which is a chordotonal apparatus, further improved by the occurrence in close proximity to it of a saclike enlargement of a trachea which serves as a resonator. Similar organs occur in pairs on opposite sides of the tibiæ of the first pair of legs in the Crickets (Gryllidæ), and seem from their structure to be auditory organs, whence the conclusion that the more simple chordotonal organs also subserve this function.

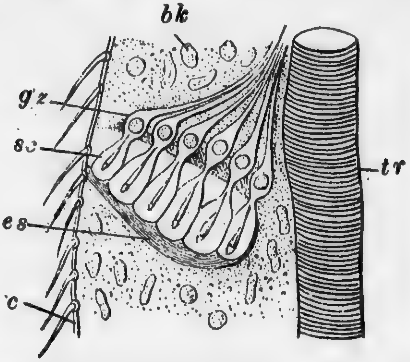

FIG. 229.—SUBGENUAL CHORDOTONAL ORGAN OF THE TIBIA OF THE SECOND THORACIC APPENDAGE OF *Isopteryx* (after GRABER from LANG).

bk = blood-corpuscles.
c = integment.
es = terminal ligament.
gz = nerve-cells.
tr = trachea.
sc = terminal hairs and sheaths.

It is interesting to note that the males of the forms provided with a tympanal organ possess the power of making a harsh or sharp chirping noise, produced in the Grasshopper by rubbing the femora of the hind legs, which are furnished on their inner surfaces with a row of fine teeth, over the strong marginal veins of the anterior pair of wings; and in the Crickets and Locustidæ by rubbing together the two anterior wings, a row of teeth upon a vein of one wing working upon a projecting smooth vein of the other. The male Cicadas also make a similar noise, the stridulating apparatus resembling that of the Grasshoppers, and in all cases it seems to be a sexual characteristic serving to attract the females.

The sexes are separate, and a more or less distinct sexual dimorphism occurs, the males being usually smaller and more slender than the females. In some cases, as in the Tussock-moth (*Orgyia*), the female lacks wings and has a very different appearance from the males, and in many Beetles the male is adorned with spines and tubercles upon the head which are but rudimentary or absent in the female. Differences in the shape of the antennæ and the presence or absence of stridulating organs also serve to distinguish the two sexes in some of the groups. In a few forms a polymorphism is produced by the failure of certain individuals to reach sexual maturity and by the assumption by them of certain special structural characteristics. Examples of such cases are afforded by the Bees, Ants, and Termites, the workers of the first two groups being immature females, while in the Termites (Fig. 237) the so-called neuters may be either males or females, always, however, immature.

The ovaries (Fig. 227, *ov*) are paired and consist of a varying but usually rather large number of tubes, which start from a common basis. At the extremity of each tube is the germ-producing region, the rest of the tube being divided into a series of chambers each of which contains an ovum surrounded by a layer of follicle-cells. Not unfrequently the chambers are arranged more or less distinctly in pairs, the lower one of each pair containing an ovum, while the upper contains a number of small cells similar in appearance to the primary germ-cells, but which serve as nutrition for the ovum which gradually absorbs them (see Fig. 20). From each ovary an oviduct arises, the two, however, soon uniting, and receiving, usually not far from the unpaired orifice, the ducts of various glands (*ag*) whose secretion serves to cause an adhesion of the ova to the structures on which they are deposited. A receptaculum seminis is usually present, and there is frequently a large pouch, partially separated from the oviducts, which receives the male organ during copulation and is termed the *bursa copulatrix* (*bc*). The genital orifice is situated on the ventral surface of the ninth abdominal segment and is usually surrounded by a number of papillæ, or sometimes by long processes, which serve as ovipositors and are to be regarded simply as processes of the segments from which they arise and not as modified limbs.

The testes are also paired, each being composed of a number of separate spherical or tubular portions. The ducts from these various portions on each side unite to form a vas deferens which may dilate into a vesicula seminalis and then, uniting with its fellow of the opposite side, forms the ductus ejaculatorius. Occasionally the vesicula is unpaired arising from the point of union of the two vasa deferentia, and very frequently accessory glands occur. The ductus ejaculatorius opens usually on the ventral surface of the tenth abdominal segment, and projections of the body-wall in the vicinity of the orifice form a groove or tube through which the spermatozoa, usually united into spermatophores, are introduced into the bursa copulatrix of the female.

Parthenogenesis occurs as a normal process in certain Insects, though always associated with true sexual reproduction. Examples of it are found in certain Coccidæ (*Aspidiotus*) and in some of the Gall-wasps (Cynipidæ), the fertilized ova producing both males and females, while in the Bees, for example, in which both fertilized and unfertilized ova are deposited, the latter give rise to drones or males alone, while workers or queens, i.e. the females, develop from the fertilized ova. Occasionally heterogony occurs, as in the Plant-lice (Aphidæ). These forms under favorable conditions of temperature and food produce viviparously usually wingless individuals, not, however, from true ova, but by a process which may rather be compared to internal budding, as in the Rediæ of certain Trematoda. Generation after generation of such individuals may be produced during the summer, but on the

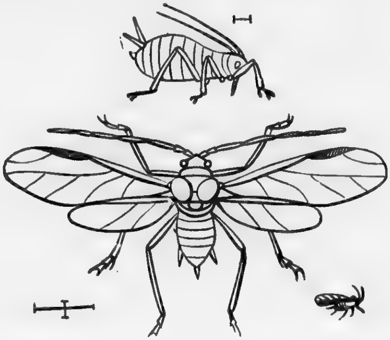

FIG. 230.—*Aphis mali*, WINGED AND WINGLESS FORMS (from Packard).

approach of cold weather or on the exhaustion of the food-supply males and females appear by which true fertilized ova are produced, and from these, surviving the winter, viviparous heterogonous females develop.

In the genus *Phylloxera*, which has played such havoc on grape-vines in France, a greater complication of generations occurs. A winter egg, which has survived beneath the bark of the vine, gives rise to wingless forms which migrate to the roots, and there produce numerous generations. After a time winged forms appear which ascend from the roots, and, reproducing parthenogenetically, increase rapidly in number and serve to distribute the species over wider areas. Certain of these produce small ova from which males develop, and others larger ones which give rise to females, both sexes being destitute of both wings and digestive tract, and by these forms the fertilized winter eggs are produced.

In certain flies (*Miastor*, *Cecidomyia*) pædogenesis occurs, the female reproductive organs becoming mature while the insect is still in the larval stage, and the ova, developing parthenogenetically within the body, give rise to another generation of larvæ. This process may be repeated several times, the last generation of larvæ developing into the adult form (see Fig. 29).

The more primitive Insects, the Thysanura and Collembola, leave the egg in a form resembling the adult, differing from it only in size and in the immaturity of the reproductive organs, and pass through no marked metamorphosis during their post-embryonic development. Such forms are termed *ametabolic*. A similar absence of metamorphosis is found in certain forms degenerated by parasitism and lacking wings, but these have evidently descended from winged forms which passed through a certain amount of metamorphism, so that the ametabolism is secondary and should be distinguished from the primitive ametabolism of the Thysanura. In the majority of winged forms, however, a more or less pronounced metamorphosis occurs. In the simpler cases the young are distinguishable from the adults by the absence or but slight development of the wings, which become larger after successive moults, the adult form being thus gradually acquired. In these cases of gradual metamorphosis the habits of the adult and larva are similar, but where they differ greater changes result, leading to *hemimetabolism*. This occurs, for instance, in the Fish-flies (Ephemeridæ) and Dragon-flies (*Libellula*), in which the larvæ are adapted for an aquatic life and possess tracheal branchiæ (Ephemeridæ) and other features which are lost, either gradually by successive moults or suddenly at the last moult, the adult winged Dragon-fly, for instance, issuing from a peculiar aquatic larva with the merest rudiments of wings.

Finally, a large number of forms are *holometabolic*. In such cases the habits of the larvæ are different from those of the adults; for instance, the larvæ of the Butterflies, the caterpillars (Fig. 231), are wormlike creatures with powerful jaws feeding on plant-tissues, while in the adults the mouth-parts are adapted for sucking. The transformation from the larva to the adult is accomplished by the intervention of a resting stage or *pupa*, during which no nutrition is taken, and when the transformation takes place the fully-developed insect or *imago* issues from the ruptured skin of the pupa. The pupa varies considerably in form in different groups, in some being enclosed in a silken case manufactured by the larva before the last moult and termed a cocoon. In some cases the adult appendages project from the body of the pupa (*pupa libera*), but in other cases they are united with the surface of the body and but indistinctly visible (*pupa obtecta*), an arrangement usually found in the Butterflies, whose pupæ, owing to their frequent brilliant coloration, are termed *chrysalids*. a term which has been somewhat incorrectly extended to the mummy-like pupæ of other forms.

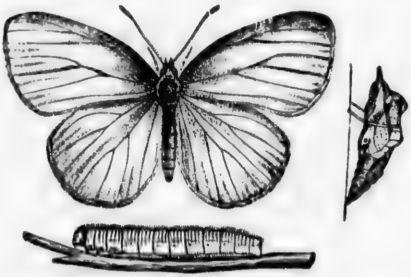

FIG. 231.—LARVA, PUPA, AND IMAGO OF *Pieris oleracea* (from RILEY).

Finally, in some of the two-winged flies the pupa is enclosed within the last larval skin, possessing then a cylindrical form without any indication of the adult limbs (*pupa coarctata*). A metamorphosis in which a distinct pupa-stage occurs is said to be "complete" in contradistinction to the hemimetabolic form frequently spoken of as "incomplete."

Mention should be made here of the dimorphism or polymorphism which occurs in certain adult Insects. It has already received passing mention (p. 497), but in addition to the frequently-occurring sexual dimorphism there occurs in forms which live together in colonies a polymorphism associated with a division of labor on the parts of the members of the colony. Thus in the Bees there are found the drones or males with heavy bodies, the queen or female, as large as the drones but with a much more slender body, and the workers, which are sterile females distinguished by their smaller size and by other features, such as a peculiar modification of the tibias of the last pair of legs which adapt them for the collection of pollen from the flowers which they visit. Among the Ants a similar trimorphism occurs, males, females, and neuters or workers constituting the colony; and in some tropical forms the workers are of two kinds, namely, ordinary workers with small heads and mandibles, and soldiers with large heads and strong prominent mandibles, whose functions are indicated by the popular name applied to them, though guards would perhaps be more appropriate. Finally, among the Termites, popularly known as the White Ants, four forms, i.e., males, females, workers, and soldiers, also occur.

In certain Butterflies a peculiar form of dimorphism or trimorphism termed "seasonal dimorphism" occurs, an excellent example of it being offered by the American *Papilio Ajax*, of which there have been described three distinct varieties, differing markedly in coloration both in the males and the females, and distinguished as the varieties *Walshii*, *Telamonides* and *Marcellus*. From chrysalids which have passed the winter there hatch out in the early days of spring forms belonging to the variety *Walshii*, and somewhat later, from those whose development has been retarded, the *Telamonides* forms. During the early part of summer the *Walshii* forms die out and a little later the *Telamonides* also disappear, both forms previously, however, depositing ova, most of which develop into larvæ and chrysalids and hatch out in the later months of summer as the *Marcellus* form, whose ova, again developing into chrysalids, pass the winter in that state, and give rise in the following spring successively to the *Walshii* and *Telamonides* forms. The three varieties are evidently produced by influences acting upon the chrysalis and differing according to the season, perhaps according to temperature, whence the distinguishing name applied to this form of dimorphism, which is also said to occur in certain Spiders.

1. Subclass **APTERYGOTA.**

The members of this subclass are all small and do not possess wings, the absence of these structures being a primitive feature and not due to degeneration resulting from parasitism or other causes. In some forms rudiments of abdominal limbs are present in the adults, and there is no metamorphosis in the post-embryonic development (primary ametabolism).

1. Order **Thysanura.**

The Thysanura or Bristle-tails possess ten abdominal segments, the terminal one bearing two- or three-jointed hairlike processes, whence the name applied to the order. The body in some forms (*Lepisma*) is covered with scalelike hairs giving it a silvery-gray appearance, but in other cases these are wanting. The antennæ vary in length, but are always simple cylindrical structures, the terminal joint in some forms (*Campodea*) bearing a peculiar bilobed structure supposed to be sensory, and the mouth-parts are adapted for biting purposes and are usually well developed. The first abdominal segment in some forms bears a pair of indistinctly-jointed appendages, probably rudimentary limbs, and a number of the succeeding segments in *Campodea* bear spurlike processes, also supposed to be limbs and recalling the spurs of *Scolopendrella*, especially as protrusible glandular structures, comparable perhaps to crural glands, occur in association with them in some forms.

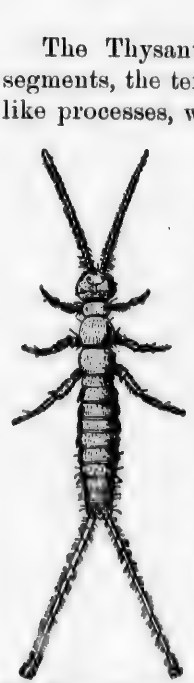

FIG. 232.—*Campodea staphylinus* (after LUBBOCK from HUXLEY)

The nervous system shows but little concentration, eight abdominal ganglia occurring in *Lepisma*, and eyes are usually present, being in some cases compound. The stigmata vary in number, being usually ten, though in *Campodea* they are reduced to three, and the tracheæ in this same form are interesting in being destitute of longitudinal and transverse anastomoses.

Lepisma is frequently found in houses, in attics and similar places, feeding upon woollen, linen, and other fabrics, but also on meal or sugar. *Campodea* (Fig. 232), on the other hand, is to be found under stones or dried leaves and is a small white form, by no means uncommon.

2. Order **Collembola.**

The Collembola are distinguished from the Thysanura by the abdomen consisting usually of but six segments, and in some cases the number is even smaller. The body in *Podura* is covered with scales, and the terminal segment of the body is usually provided with two processes which may be bent up underneath the abdomen and then suddenly extended, propelling the insect to a considerable distance. These structures are absent in the adult *Anurida*, but occur in young specimens, and their occurrence and function have suggested the popular name of Spring-tails applied to the order. Neither abdominal appendages nor coxal glands occur, but the first segment bears a peculiar organ, having in *Anurida* the form of a saccular protrusion, which is probably adhesive in function. The antennæ are usually short, and bear in some forms an antennal sense-organ similar to that of *Campodea*; the mouth-parts are biting, but frequently much reduced in size.

The nervous system is usually much concentrated, there being in *Anurida* but three postoral ganglia situated in the thorax, the abdominal ganglia having evidently fused with the last thoracic. Simple eyes are present in varying numbers, but compound eyes never occur. A peculiar organ lying behind the bases of the antennæ, and hence termed the post-antennal organ, occurs, and has been supposed to be a sense-organ, but further information is required concerning it. Tracheæ are usually present, though quite wanting in *Anurida*.

The genus *Podura* is to be found, sometimes in considerable numbers on the surface of standing water in the early spring, while other forms occur in damp earth or under bark. *Anurida* is found upon the seashore underneath stones just above tide-mark.

II. Subclass **Pterygota.**

The members of the subclass Pterygota are, as the name indicates, typically provided with wings, though in a comparatively few cases these structures may have disappeared through degeneration due to parasitic habits, or through special adaptation to certain conditions of life, as in the neuters of the Ants and Termites. In nearly all cases the larvæ differ in form from the adults, and various grades of metamorphosis are found.

1. Order **Dermaptera.**

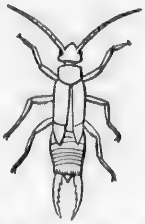

Fig. 233.—*Labia minor* (after Leunis).

The Dermaptera or Earwigs (Fig. 233) are usually small insects which resemble not a little the Thysanura. The abdomen terminates in a pair of forceplike processes termed cerci, their shape suggesting the generic name *Forficula*, applied to certain members of the order. The anterior wings are small and chitinous and serve as covers for the protection of the posterior pair, which are larger, membranous and veined, and when at rest are folded longitudinally like a fan, and in addition twice transversely, so that they are almost completely hidden by the scalelike anterior pair. The antennæ are long and filiform, and the mouth-parts adapted for biting. The Earwigs are terrestrial forms and pass through a gradual metamorphosis. In many respects they approach nearer the Thysanura than any other insects, and are related rather closely to the succeeding order.

2. Order **Orthoptera.**

In this order, which includes the Locusts, Grasshoppers, (*Caloptenus*), Crickets (*Gryllus*), Cockroaches (*Periplaneta*), and other forms, the mouth-parts are adapted for biting and the last segment of the abdomen bears two-jointed cerci. The anterior wings form, as in the Dermaptera, covers for the posterior pair and are chitinous plates; the posterior ones are, on the other hand, membranous and the veins are for the most part arranged longitudinally, so that when at rest the wings are folded like a fan, though in some forms, such as the Crickets, in which the anterior wings are short, a transverse fold also occurs. In the female Cockroaches the anterior wings are very small, and the posterior ones wanting, and in the Walking Stick (*Diapheromera*)—so named from its resemblance to a green or dead twig—both pairs are entirely wanting.

The antennæ are usually long and filiform, and the legs strong and adapted to a terrestrial life, some forms, such as the Cockroach, being exceedingly active. In the Grasshoppers, Locusts, and Crickets the femora of the last pair of legs are greatly enlarged and very muscular, serving for jumping, while in the Mole-cricket (*Gryllotalpa*), which burrows in the ground, the anterior pair is greatly enlarged and adapted for digging.

As in the Earwigs, the metamorphosis is gradual.

3. Order **Ephemeridæ.**

The Ephemeridæ, or May-flies (Fig. 234), are characterized by the remarkable brevity of their existence in the imago-stage, some forms existing but for a few hours, while others live for several days, the existence being merely long enough to ensure the accomplishment of the reproductive acts. The body is elongated and terminates in two or three elongated hairlike cerci, and on the thorax there are borne usually two pairs of wings, of which the anterior pair is considerably larger than the posterior. The antennæ are short, and the mouth-parts adapted for biting, though usually much reduced, since the imago takes no nutrition during its short existence. The first pair of legs is usually slender and directed forwards, being of little use in locomotion. An interesting structural peculiarity is the occurrence of paired reproductive ducts which open by separate

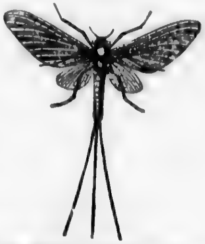
FIG. 234.—*Potamanthus marginatus* (from PACKARD).

pores instead of uniting as they do in the majority of Insects.

The larvæ are aquatic and provided with tracheal branchiæ (see Fig. 226), recalling, except for these structures, the Thysanura. By a series of moults the adult stage is gradually acquired, the wings appearing in what is termed the subimago stage, a final moult being necessary before maturity is reached. The metamorphosis is thus incomplete.

The genus *Ephemera* is of frequent occurrence in the neighborhood of lakes and ponds, sometimes occurring in enormous numbers.

4. Order **Odonata.**

The members of this order, the Dragon-flies, are elongated forms with two pairs of nearly equal, abundantly-veined wings of usually large size, all the forms being excellent fliers and seeking their prey in the air. The head is united to the thorax by a narrow stalk which permits extensive rotation of the head, and the abdomen, terminating in two unsegmented platelike cerci, is long, and in the large Dragon-flies, *Æschna* and *Diplax* (Fig. 235), and in the brightly-colored *Agrion* very slender, though somewhat stouter in the genus *Libellula.* The antennæ are very small and the mouth-parts adapted for biting, while the legs are slender, the anterior pair being directed somewhat forwards so as to serve for grasping the prey. The lateral compound eyes are very large, meeting on the dorsum of the head, and in front of them are situated a pair of small ocelli.

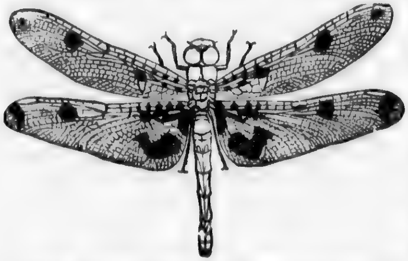

FIG. 235.—*Diplax elisa* (from PACKARD).

The larvæ are aquatic and are characterized by the remarkable development of the labium, which is very much enlarged, terminating in two powerful jaws and provided with a hinge, so that it can be flexed so as to lie beneath the head or suddenly thrust out to capture the unwary prey. This apparatus is termed the "mask." Respiration is carried on by tracheal gills, consisting in *Agrion* of three leaflike processes situated at the posterior end of the body, and also by the terminal portion of the intestine, into which water is taken and which is abundantly supplied with tracheæ. The water can be forcibly expelled from the intestine, serving to propel the insect through the water if it so desires. The metamorphosis is incomplete.

5. Order **Plecoptera.**

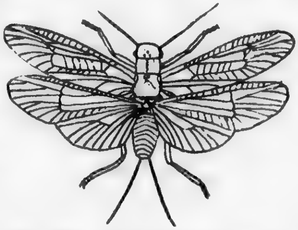

FIG. 236.—STONE-FLY, *Perla*.

The Plecoptera, or Stone-flies (Fig. 236), are found in the vicinity of water and have a somewhat elongated body, frequently terminating in two long cerci (*Perla*). The antennæ are long and filiform and the mouth-parts adapted for biting, while the legs are strong and used for walking. Two pairs of wings occur almost equal in size, but lacking the complicated venation found in the Odonata, and when at rest lie flat upon the abdomen, completely concealing it. The larvæ are aquatic, and are usually to be found in considerable numbers under stones in swiftly-running streams. They recall the Thysanura in their appearance, and possess tracheal branchiæ on the under surface of the thorax, which in some forms are retained in the adult. The metamorphosis is gradual or incomplete according as these structures are or are not retained in the imago.

6. Order **Corrodentia.**

The members of this group possess biting mouth-parts and are sometimes destitute of wings. The Termites, or White Ants, live in colonies and show a polymorphism. The males and females, termed kings and queens (Fig. 237, *A*, *B*), are at first provided with large wings resembling those of the Plecoptera, but after the marriage flight settle to the ground and become wingless. The workers select from the many pairs one for each nest, the remaining unselected ones soon dying. The neuters are of two sorts: the workers (Fig. 237, *C*), pale in color and with comparatively small heads and mandibles, and the soldiers (Fig. 237, *D*), in which the head is very large and dark colored and carries a pair of large mandibles. Both these forms are destitute of eyes, and are to be regarded as individuals which have not passed beyond the larval stage, being potentially either males or females with the reproductive organs, however, undeveloped. The young larvæ resemble Thysanura in their general form and are cared for and fed by the workers. Those forms which are destined to become kings and queens are nursed for a longer time than the others, and progress further in their development, being really the only members of the colony which reach the imago state.

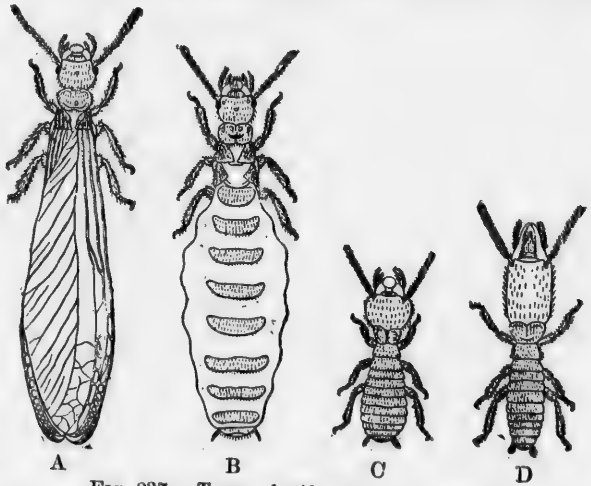

FIG. 237.—*Termes lucifugus* (from LEUNIS).
A, winged male; *B*, female after loss of wings; *C*, worker; *D*, soldier.

The Termites shun the light, and the American species are chiefly found in rotten wood, upon which they feed, excavating burrows within it. In some cases they prove very destructive to the woodwork in houses, eating away the interior of the wood and leaving eventually only a thin shell in place of the originally solid beam. The African species builds large clay mounds from three to four metres in height, tunnelled by a somewhat complicated system of chambers, galleries, and storehouses.

To this group belong also the *Psocidæ* and the *Mallophaga.* The former are small forms found upon the leaves of various trees and occasionally in houses. They do not show polymorphism and are usually provided with wings, though the genus *Atropos*, not uncommon in books which have remained long undisturbed, lacks them. The Mallophaga are all destitute of wings and are parasitic, living upon the bodies of birds (*Liotheum*), whence they are usually termed the Bird-lice. They feed upon the feathers and are comparatively active in their movements. A few forms occur on mammals, e.g. *Trichodectes* on the dog.

The larvæ of all these forms resemble the adults except in size and in the absence of wings, and the metamorphosis is gradual. Since the Mallophaga are destitute of wings in the adult condition they may properly be said to be secondarily ametabolic.

7. Order **Thysanoptera.**

The Thysanoptera are small Insects which live upon the leaves of various plants, which they pierce for the purpose of obtaining nutrition, and sometimes are very injurious to wheat, clover, and other cultivated plants. The wings are narrow, but imperfectly veined, and with the edges fringed with numerous slender hairs ; they are, however, occasionally wanting. The antennæ are short and filiform and the mouth-parts intermediate between the biting and the sucking type. The mandibles are reduced to styletlike piercing-organs and are enclosed within a tubular proboscis formed by the fusion of the labrum with the maxillæ and labium, both of these last appendages retaining their palps and showing usually their typical parts. The legs are adapted for rapid locomotion and are peculiar in that the terminal joint of the tarsus, instead of bearing ungues, is provided with a protrusible sac which serves for adhesion ; on account of this peculiarity the order is sometimes known as the *Physapoda.*

The larvæ except for the absence of wings are closely similar to the adults and the metamorphosis is gradual, though the tendency towards the development of a distinct pupal stage is shown by the fact that the last larval stage takes no nourishment. The genus *Phlœothrips* is characterized by the last abdominal segment being tubular in form, while *Thrips* possesses in the female forms an ovipositor composed of four valvelike pieces.

8. Order **Rhynchota.**

The members of this order are divisible into two groups, the *Heteroptera* and *Homoptera*, according to the character of the anterior wings. In the Heteroptera, which includes the majority of forms popularly known as Bugs, the basal partions of the anterior wings are chitinous, while the tips are membranous, the posterior wings being entirely membranous. A typical member of this group is the common Squash-bug (*Anasa*, Fig. 238, *A*), and other examples are the Water-boatman (*Notonecta*), the large Water-scorpion (*Belostoma*), and the slender Water-scorpion (*Ranatra*), all of which are of frequent occurrence in ponds, swimming powerfully beneath the water by means of the flattened posterior legs which serve as oars, the anterior pair being directed forwards and serving for grasping the prey. The Water-measurer or Water-spider (*Hydrometra*) is also very common in ponds, darting about upon the surface in search of prey, a habit which also characterizes the genus *Halobates*, which lives upon the surface of the ocean and is found many miles from land. Some members of the group are entirely destitute of wings, as for example the Bedbug (*Cimex*) and the Louse (*Pediculus*).

In the Homoptera the wings are both membranous, the anterior pair being larger than the posterior, and, as in the other group, are sometimes wanting. The *Cicada* is a member of this group, as are also the Aphidæ, or Plant-lice (Fig. 230), so frequent in green-houses and upon various uncultivated plants whose juices they suck, a habit also shared by the nearly-allied Coccidæ, including the scale-insects (*Aspidiotus*) and the Mealy-bugs (*Dactylopius*), both of frequent occurrence on cultivated plants, the former sometimes doing no little damage to apple-trees. The remarkable heterogony of these forms has already been described (p. 498).

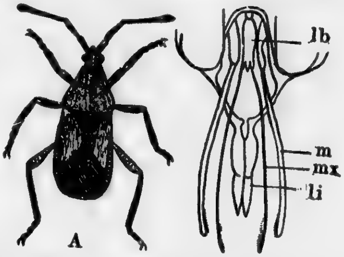

FIG. 238.—*A*, *Anasa tristis*; *B*, MOUTH-PARTS OF *Nepa cinerea* (after SAVIGNY from OWEN).
lb = labium.
li = tongue.
m = mandibles.
mx = maxillæ.

In both the suborders the mouth-parts are adapted for piercing and sucking. The labium (Fig. 238, *B*, *lb*) is prolonged into a slender, usually four-jointed process, grooved upon its upper surface, the groove being convertible into a tube by the closure over it of the long slender mandibles (*m*) and maxillæ (*mx*) which form long slender needlelike piercers. The antennæ are usually short and filiform, though in some of the Heteroptera they may be almost as long as the body.

Many of the Rhynchota are provided with glands which secrete an offensive fluid, e.g. in *Cimex* and *Anasa*, and in the Coccidæ wax-glands are also abundantly present, producing a secretion which may cover the body with waxen scales, or in some cases form a wool-like mass covering the greater part of the abdomen (*Pemphigus*). The Aphidæ also possess as a rule upon the antepenultimate abdominal segment a pair of tubular elevations or papillæ from which a sweet secretion issues, the so-called "Honey-dew," which covers the leaves and stems of the plants upon which the Insects live, and is eagerly sought for by various Insects, more especially by Ants.

The larvæ of the Rhynchota as a rule resemble the adults even to the structure of the mouth-parts, and the metamorphosis is consequently gradual. The *Cicada* forms, however, an exception to this rule, the larva occurring beneath the surface of the ground and living upon the roots of trees. It becomes transformed into a pupa, which, however, continues to lead an active existence, becoming quiescent only a short time before the moult which results in the formation of the imago, very different in appearance from the pupa. The metamorphosis here approaches the complete type.

9. Order **Coleoptera.**

The order Coleoptera includes the Beetles and is richer in species than any other order of animals. The members of the group are characterized by the anterior wings being converted into hard chitinous plates, the elytra, which cover in and protect the posterior membranous wings and the abdomen, being short only in a few forms, such as the Burying-beetles (*Necrophorus*), in which the tip of the abdomen remains exposed, and the Staphylinidæ, or Rove-beetles, and *Meloë*, in which they cover only the more anterior portions of the abdomen, the posterior wings in the last-named form being wanting, as they may also be in some of the Weevils. Occasionally, as in the Fireflies (*Lampyris*), the elytra are but slightly thickened, and in some forms they may be completely fused together.

The antennæ vary greatly in shape, being usually filiform and sometimes very long, as in the Boring-beetles (*Monohammus*, *Clytus*, *Saperda*, etc.), though occasionally, as in the Lamellicorn beetles (*Melolontha*—the June Bugs and *Cotalpa*, Fig. 239), the terminal joints are flattened and folded together like the leaves of a book. The mouth-parts (Fig. 225) are in all cases adapted for biting, and the legs for locomotion. In the Lady-bugs (*Coccinella*) the tarsus consists of but four joints, one of which is rudimentary, while in the Weevils (Curculionidæ), in which the anterior part of the head is pro-

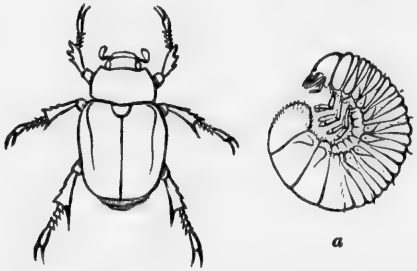

FIG. 239.—*Cotalpa lanigera* AND ITS LARVA (*a*) (from PACKARD).

longed into a cylindrical snoutlike process at the extremity of which is the mouth, in the Boring-beetles, and in the Potato-beetle (*Doryphora*) it is formed of five joints, one of which is exceedingly small. In other forms, such as *Meloë* and the Blister-beetles (*Lytta*), the tarsi of the two anterior pairs of legs are five-jointed and those of the last pair four-jointed, and in others again, such as the Fireflies, the Click-beetles, (Elateridæ), the Lamellicornes, the Burying-beetles and Staphylinidæ, the Water-beetles (*Gyrinus, Hydrophilus*, etc.), the Carabidæ (*Calosoma, Carabus, Harpalus, Brachinus*, etc.), and the Tiger-beetles (*Cicindela*), all the tarsi are five-jointed, and all the joints approximately equally developed.

The larvæ vary greatly in form in the different genera. In the Lady-bugs and some other forms they are Thysanuriform, the three anterior trunk-segments (corresponding to the thoracic segments of the imago) possessing each a pair of limbs, while the abdomen terminates in a pair of cerci. In some Water-beetles (*Gyrinus*) tracheal gills are present, and the larvæ of the Lamellicorns (Fig. 239, *a*) are soft-bodied eyeless white forms, characterized by a saclike dilatation of the last abdominal segment, and live beneath the surface of the ground feeding upon the roots of grasses. In the Click-beetles (Elateridæ) the body of the larva is elongated and slender and very hard, these forms being known as the wireworms and feeding, like the Lamellicorn larvæ, upon the roots of plants. In the Boring-beetles, the larvæ, which excavate burrows beneath the bark or in the wood of various trees, have the limbs almost or quite rudimentary, while maggot-like larvæ are characteristic of the Weevils.

The larva, whose life may be prolonged through several years, passes finally into a resting pupa stage of the *libera* form, resembling in the body form and the mouth-parts the imago which sooner or later issues from it. The metamorphosis is thus complete.

In the peculiar Meloid form *Sitaris* an interesting phenomenon known as *hypermetamorphosis* occurs. The first larva is Thysanuriform, and is parasitic upon the males of certain bees, passing to the female bee during copulation, and then, during the deposition of the ova in the cells filled with honey, the parasite slips upon the egg, which it consumes. It then transforms into a maggotlike second larva which lives upon the honey on the surface of which it floats, and after a time passes into a resting pseudochrysalis stage, from which a larva similar to the second one emerges, and this finally transforms into a pupa which gives rise to the adult.

10. Order **Neuroptera.**

The Neuroptera are characterized by the abundant and rich venation of their wings, in which numerous cross-veins extend between the longitudinal ones. The mouth-parts are adapted for biting, the mandibles being in some forms (*Corydalis*) very large. The lace-winged flies (*Chrysopa*) also belong to this group, as does also the Ant-lion (*Myrmeleon*, Fig. 240), whose larva excavates a funnel in loose sand, and buries itself at the bottom with only the head and powerful mandibles projecting, ready to snap up any insect which slips down the yielding sides of the trap. The larvæ are usually Thysanuriform, those of *Chrysopa* attacking Aphides, whence they are frequently termed Aphis-lions, while those of *Corydalis* are aquatic and possess tracheal branchiæ upon the abdomen. This larva is familiar to anglers as the Hellgramite. The metamorphosis is complete.

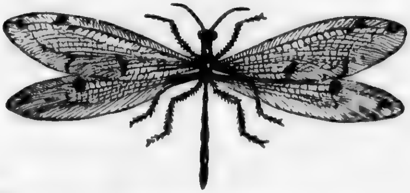

FIG. 240.—*Myrmeleon obsoletus* (from PACKARD).

11. Order **Panorpata.**

This order contains a small number of forms, the majority of which possess membranous wings resembling those of the Neuroptera, except that the cross-veins are not so numerous. The anterior part of the head is produced into a downwardly projecting snout, at the extremity of which are the small biting mouth-parts, the arrangement recalling that found in the Curculionidæ among the Coleoptera. In the genus *Pa-*

norpa, the Scorpion-fly, the abdomen terminates in a pair of forceplike processes similar to those of the Dermaptera.

The metamorphosis is complete, the larvæ differing from those of the orders already described in possessing in addition to the three pairs of thoracic legs eight pairs of abdominal proplike appendages.

12. Order **Trichoptera.**

The Trichoptera, also a small order, includes the Caddis-flies (*Phryganea*, *Anabolia*). They possess two pairs of wings, the anterior pair usually differing slightly in appearance from the posterior, which are larger and folded when at rest in a fanlike manner, the venation consisting principally of longitudinal veins, with but few transverse ones. The body and the wings are generally abundantly covered with hairs, which in some forms are scalelike. The antennæ are usually long and filiform, and the mandibles rudimentary, the maxillæ and labium forming a short sucking proboscis.

The metamorphosis is complete, the larvæ being aquatic and provided with spinning-glands with which they bind together small twigs and particles of sand to form cases within which they live. They possess tracheal branchiæ upon the sides of the abdominal segments, and the last segment bears a pair of short but stout processes which are provided with hooks. The pupa is formed within the larval case, but before transforming into the imago it leaves the case and crawls to land, where the imago emerges.

13. Order **Lepidoptera.**

This is a large order, including the Butterflies and Moths, all of which, with the exception of the females of a few forms (*Orgyia*), possess two pairs of wings covered with overlapping scalelike hairs, and with but few transverse veins. When at rest the wings are rarely folded, but are either held erect, as in the Butterflies, or lie one over the other, resting upon the abdomen. The body, like the wings, is covered with hairs or scales.

The antennæ differ considerably in shape in different forms, being in the Butterflies usually club-shaped, while in male moths they are frequently featherlike, though more simple or filiform in the females. The mouth-parts are adapted for sucking, forming in most cases a long tube, which, when not in use, is coiled into a helix. In the smaller members of the group (Microlepidoptera), which are in many respects the most primitive and include such forms as the Clothes-moth (*Tinea*), the moth of the Apple-maggot (*Carpocapsa*), the leaf-rollers (Pyralidæ), etc., the sucking arrangement is by no means perfect, the mandibles being present, and the maxillæ and labium resembling in structure the corresponding parts in biting insects, except that the two inner terminal plates of the labium are united to form a short tube. In the higher forms (Macrolepidoptera), however, the mandibles (Fig. 241, *mn*) are quite rudimentary and the labium is much reduced in size, though its palps (*lp*) are frequently large and well developed. The sucking-tube is composed of the two maxillæ (*m*) which are produced into two long filaments grooved on their mesal surfaces, and by their apposition the tube is formed.

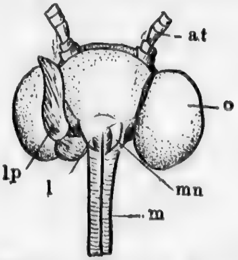

FIG. 241.—HEAD OF MOTH, *Sphinx ligustri*, SHOWING MOUTH-PARTS (after NEWPORT).

a = antennæ.
l = labrum.
lp = labial palp; that of left side removed.
m = maxillæ.
mn = mandible.
o = eye.

The metamorphosis is in all cases complete, the larvæ being wormlike structures known as caterpillars. Their mouth-parts are adapted for biting, and they live for the most part upon the leaves of various plants, frequently accomplishing much destruction. This is especially the case with the Tent-caterpillar (*Clisiocampa*), which lives in colonies enclosed within a web which is extended from twig to twig as the leaves are gradually eaten; various kinds of trees suffering from its ravages. The shade-trees in cities, especially the Horse-chestnut, are sometimes greatly injured by the caterpillar of the Tussock-moth (*Orgyia*), and the larvæ of the common white Cabbage-butterfly (*Pieris*) feed upon the leaves of the Cabbage; many other similar examples might be given. A few of the Microlepidoptera possess aquatic larvæ, but they form exceptions. In the typical caterpillar there are, in addition to the three pairs of thoracic legs, five pairs of short stout prop-legs situated upon the third, fourth, fifth, sixth, and tenth abdominal segments, and the body may be covered with hairs of various lengths, as in the larvæ of many moths (e.g. the Woolly Bear, *Spilosoma*), or may possess spiny processes, as in the larvæ of the Mourning-cloak Butterfly (*Vanessa*) which feeds on the Willow, or variously-shaped tubercles, as in the American silkworm (*Telea*) and the *Cecropia* larva. In one group of moths, the Geometridæ, but two or three pairs of prop-legs occur, situated on the more posterior segments, and in progression these forms draw these legs up close to the thoracic limbs, throwing the intervening portion of the body into a loop, whence the terms "measuring-worms" or "loopers" often applied to them. In rare cases, as in a few Microlepidoptera, the larva is without feet and maggotlike.

The pupa or chrysalis is of the *obtecta* variety, and is frequently enclosed within a silken case termed the cocoon, spun by the larva whose salivary glands are converted into spinning-glands. A cocoon is more generally present in the Moths than in the Butterflies, whose chrysalids are suspended by a patch of silk to which the hind end of the pupa is attached or may be in addition slung in a silken loop passing round the body near the middle (Fig. 231).

14. Order **Hymenoptera.**

The Hymenoptera possess four membranous wings, with comparatively few veins and not covered with scales or hairs but transparent, the anterior pair being usually larger than the posterior. The abdomen is sometimes broadly attached to the thorax, as in the Saw-flies (Tenthredinidæ), but more usually the anterior one (Bees) or two (Ants) abdominal segments are very narrow, so that the abdomen seems to be attached by a stalk. The females possess ovipositors which may be retractile and provided with a poison-gland, forming efficient organs of offence and defence, as in the Ants, Bees, and Wasps, or else long and slender and but partially retractile and destitute of a poison-gland, as in the Saw-flies, Gall-flies, and Ichneumonidæ.

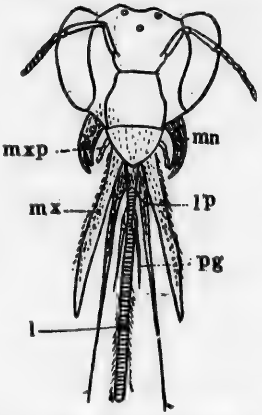

FIG. 242.—MOUTH-PARTS OF BEE, *Anthophora* (after NEWPORT from GEGENBAUR).
l = glossa.
lp = labial palp.
mn = mandible.
mx = maxilla.
mxp = maxillary palp.
pg = paraglossa.

The mouth-parts are adapted partly for biting and partly for licking. The mandibles (Fig. 242, *mn*) are well developed and fitted for biting in all forms, and in the Tenthredinidæ the maxillæ are also like those of biting insects, while the inner of the two terminal plates of the labium are united to form a tube, the outer plates remaining separate. In the Bees and Wasps the maxillæ (*mx*) become elongated and are no longer adapted for biting, and the inner terminal plates of the labium are fused together to form a long tonguelike structure, the *glossa* (*l*), the outer plates forming what are termed the paraglossæ (*pg*). The entire apparatus is adapted for biting and also for licking up the honey contained in the nectaries of flowers.

The great majority of forms are solitary, but a few Bees (*Apis*, *Bombus*) and Wasps (*Vespa*, *Sphex*) and the Ants (*Formica*, *Camponotus*) form social aggregations with more or less pronounced polymorphism, to which reference has already been made. The Gall-flies (*Cynips*) lay their eggs upon the leaves or stems of plants, at the same time injecting a poison which causes a proliferation of the plant-tissues, forming a gall in the interior of which is the larva of the insect; while many forms, such as the Ichneumon-flies, *Proctotrupes*, *Pteromalus*, *Microgaster*, etc., are parasitic in their larval stage, the eggs being deposited in or upon the bodies of the larvæ of other insects, a very decided check being exerted upon the larvæ of injurious insects, such as the Cabbage-butterfly, by these forms.

The larvæ of the Tenthredinidæ, for example that of the Pear-slug (*Selandria*), which feeds upon the leaves of the pear-tree, resemble the caterpillars in possessing prop-legs, of which there are as many as eight pairs. In the majority of forms, however, owing to parasitism or to being in contact with an abundant supply of nutrition stored up by the parents (Bees, Wasps) or to being fed and cared for by the workers among the Ants, the larvæ are maggotlike and almost or entirely destitute of legs. The metamorphosis is complete, the pupa being a *pupa libera*.

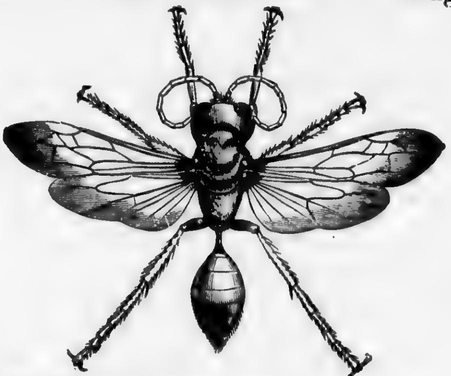

FIG. 243.—*Sphex ichneumonea* (from PACKARD).

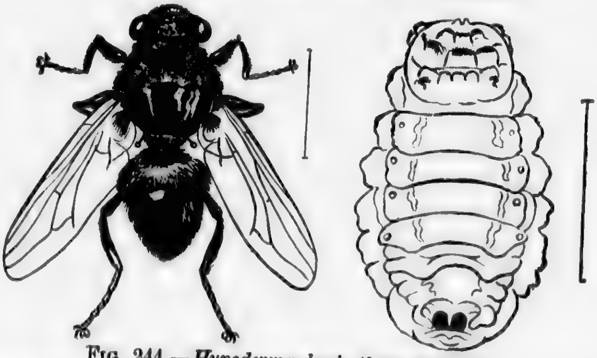

FIG. 244.—*Hypoderma bovis* (from PACKARD).

15. Order **Diptera**.

In this order, as the name indicates, but two wings are present (Fig. 244), which are those of the mesothorax, the metathoracic pair being usually represented by a pair of club-shaped bodies on the sides of the segment, termed *halteres* or balancers. The wings are always transparent and the veins by no means abundant. In a few forms, such as the Sheep-tick (*Melophagus*) and the Fleas (*Pulex*), the wings are entirely wanting in harmony with the parasitic habits which these forms possess, but they form exceptions to the general rule.

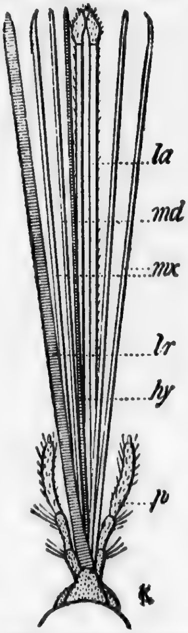

FIG. 245.—MOUTH-PARTS OF A GNAT, *Culex*, THE LABRUM TURNED TO ONE SIDE (from HERTWIG).

hy = hypopharynx, a process of labium.
la = labium.
lr = labrum.
md = mandible.
mx = maxillæ.
p = maxillary palp.

The mouth-parts are adapted for sucking and also for piercing; the labrum (Fig. 245, *lr*) and labium (*la*) are prolonged into grooved processes, forming together a tube within which lie, in the female Mosquitoes (*Culex*) and Gadflies (*Tabanus*), two pairs of elongated needlelike rods which represent the mandibles (*md*) and maxillæ (*mx*), to which a fifth unpaired stylet may be added which arises as a growth from the lower wall of the pharynx (*hy*). In other forms the maxillæ only have the acicular form, the mandibles fusing with the labrum, and in all cases the maxillary palps are present, while the labial palps are undeveloped. In the ordinary House-fly (*Musca*) the extremity of the sucking-tube is expanded into a disklike structure, and in all forms the salivary glands open near the extremity of the tube.

The larvæ are usually maggotlike (Fig. 244), entirely destitute of feet, and in some forms the head even is indistinguishable. The metamorphosis is complete, the pupa being in the Mosquitoes active, swimming about in water, though more usually it is incapable of motion, and enclosed within the last larval skin, thus belonging to the *coarctata* variety.

Development and Affinities of the Insecta.—The early stages of Insect development cannot be discussed here, belonging more properly to text-books of Embryology, but mention should be made of the remarkable phenomenon which occurs during the transformation from the pupal to the imaginal conditions in those forms whose metamorphosis is complete. In describing the development of the Acarina it was pointed out that during the transition from one stage to the next a histolysis and subsequent regeneration of certain parts of the body occurred. In the holometabolic Insects the same process occurs during the pupa stage, the larval hypodermis, the majority of the muscles, and the entire digestive tract and its appendages undergoing degeneration, and being absorbed and digested by the blood-corpuscles, the parts being formed anew from patches of cells present in the larva and known as *imaginal disks.* The histolysis and regeneration proceed *pari passu*, so that the identity of the various organs is preserved throughout the process. The imaginal discs are to be regarded as portions of the original anlagen of the various organs which have remained during larval life in an embryonic condition, springing into activity and completing their development during the pupal stage.

As regards the affinities of the various orders of the Pterygota, it may be pointed out that the frequent occurrence of Thysanuriform larvæ indicates a descent from Apterygote ancestors, and those orders which present larvæ of a wormlike or maggotlike form are in all probability the most highly specialized. It is in these cases that the complete metamorphosis occurs, and it is self-evident that the gradual and incomplete metamorphoses are more primitive than the complete. Indeed all metamorphosis depends upon the differences in habit and structure of the larva and imago, and becomes more and more complete according as the larvæ and imagines depart more and more widely from the Thysanuriform type of structure. Consequently it may be concluded that those forms are the most primitive which retain most perfectly both in the larva and imago the Thysanurid characters. These are found most perfectly in the Dermaptera, to which both in the adult and larval stages the Corrodentia (so far as they have not become modified by parasitism) and the Orthoptera seem closely related, and it is interesting to note in this connection that the earliest Insects known from the Palæozoic rocks seem to have been closely related to the recent group of the Orthoptera.

Another order which has retained Thysanuran characters in the larva, though the imagines are more highly specialized than are those of the Dermaptera, is that of the Thysanoptera, whose habits and mouth-parts indicate affinities with the Rhynchota, these two orders together forming a second group traceable back to the primitive Pterygota.

A third group starts with the Ephemeridæ, which lead up to the Odonata, the larvæ of the latter having, however, become greatly specialized, the resemblances being most marked in the adults, and are indicated by the character of the wings and by the mouth-parts. More distantly related are the Neuroptera with Thysanuriform larvæ, probably to be regarded as a group which has undergone a development parallel to that of the Ephemeridæ and Odonata, the relationship being traceable back to an ancestor common to it and the Ephemeridæ. To this group may also be referred the Plecoptera.

A fourth group includes those forms in which the larvæ are provided with prop-legs, secondary forms in which all indications of the Thysanurid ancestors have disappeared. Of such forms the Panorpata show relationships on the one hand with the Ephemerid group, and somewhat closely related are the Trichoptera, whose entire organization points to a close affinity with the Microlepidoptera. From the primitive Microlepidoptera two lines of descent are probably to be traced, one leading to the Macrolepidoptera and the other to the primitive Hymenoptera, the resemblance between the larvæ and the mouth-parts of the Tenthredinidæ, and those of the Microlepidoptera being very striking.

The two remaining orders, the Coleoptera and Diptera, are very highly specialized, both being holometabolic, and the temptation is to look for their ancestors in forms with a similar metamorphosis. This temptation may be justified in the case of the Diptera, whose larvæ are the most modified of all, and it is not impossible that they have descended from primitive Hymenopteran ancestors, their nearest existing relatives being the Tenthredinidæ, whose sluglike larvæ, suggest not a little the least modified Dipteran maggots. With the Coleoptera, however, the case is different, and it seems more probable that their holometabolism has been acquired quite independently of that of the other holometabolic orders. The larvæ of some beetles, notably those of the Coccinellidæ, are markedly Thysanuriform, and prop-legs do not occur in the order. To which of the groups they are to be referred it is very difficult to say, though the mouth parts and the arrangement and structure of the wings in the adults point to an affinity with the Orthoptera.

Granting a descent of the Pterygota from wingless ancestors, it becomes an interesting problem to discover the origin of the wings. Attempts have been made to show that they are modified tracheal branchiæ, a theory which necessitates the derivation of the Pterygota from aquatic ancestors. Such a derivation, however, is unsupported by any evidence at present at our disposal, it being much more probable that the immediate ancestors of the Pterygota were terrestrial, just as *Campodea* is to-day. The wings arise in the embryo as dorsal outpouchings of the meso- and metathorax, tracheæ later pushing out into them, and transient indications of outpouchings of the prothorax also occur in some embryos. It has been suggested that primarily the wings were platelike outgrowths of the thoracic segments which served to break the fall and increased the distance traversed by jumping Insects, and in support of this view the fact may be mentioned that many Apterygota are saltatorial. The limitation of the wings to the meso- and metathorax may stand in some relation to the centre of gravity of the body.

The Phylogeny of the Tracheata.—It has been the custom to unite together the Crustacea, Arachnida, and Tracheata in a single group, the *Arthropoda*, characterized by the possession of a chitinous cuticle, by the occurrence of jointed limbs, and by the masticatory organs being modified limbs; and furthermore it has been customary to consider the Arachnida and the Tracheata as closely related on account of the occurrence in both groups of tracheæ. The early processes of development in the three groups also show many points of similarity, though a closer examination shows decided differences in the details. How far convergent evolution may have operated to produce the similarities is the problem to be settled, and it can be settled only by a consideration of all the facts at our disposal which indicate the phylogeny of the various groups, a discussion which would prove entirely beyond the limits of a text-book.

It has been pointed out that the probable ancestry of the Crustacea is to be found in the Annelida, and that the Arachnida have in all probability descended from *Eurypterus*-like ancestors, which were certainly Crustacean in their affinities. Are the Tracheata then also descended from the Crustacea and from forms which possessed tracheæ? Our present knowledge of the group negatives any such supposition; it seems impossible that the Tracheata should, like the spiders, have descended from *Eurypterus*-like ancestors; it must rather be concluded that the similarities between them and the Arachnida are due to convergent evolution, the embryonic similarities to the acquisition of comparatively large amounts of food-yolk in the ova, distributed in a similar manner, and the similarities of the adult to the exigencies of a terrestrial life. The occurrence of tracheæ in both groups seems at first an important point of similarity to be accounted for only by a community of descent, but, when it is considered that in the terrestrial Isopoda tracheæ also occur in the branchial opercula, and that their occurrence in these forms is a purely secondary adaptation, without any phylogenetic significance, it is evident that their importance as indications of affinity is much reduced. It may also be pointed out that the Malpighian tubules of the Arachnida and Crustacea are endodermal, whereas in the Tracheata they are ectodermal, arising from the ectodermal hind-gut.

There is little room for doubt but that *Peripatus* is closely related to the Annelida, and its relationships to the Myriapoda are also pronounced, so that the conclusion seems inevitable that the Tracheata have been derived from Annelid-forms, and have therefore a phylogeny practically independent of that of the Arachnida. However, it is possible that the Annelid ancestors of *Peripatus* and those of the Crustacea were more or less closely related, and that certain of the general similarities of all the three groups are thus to be accounted for, though to what extent we are not at present in a position to judge. One point, namely, the occurrence of compound eyes of similar structure in both groups, seems worthy of consideration, since it seems to be unexplainable by this hypothesis and to be a remarkable instance of convergent evolution. It is to be noticed that the most primitive Insects, the forms through which affinities to the Crustacea if they exist must be traced, are as a rule provided only with simple eyes, a condition repeated in the eyes of Insect larvæ—a fact which indicates that the compound eyes are structures which were not characteristic of the primitive Insects, but have developed within the limits of the group and can therefore have no phyletic connection with the compound eyes of the Crustacea. Adding to this fact the independently-developed tendency to form compound eyes seen in certain Annelida and Pelecypod Mollusks, it seems probable that notwithstanding their remarkable structural similarities the compound eyes of Crustacea and Insects have been independently acquired. Instead, therefore, of uniting the three groups together as a type Arthropoda equivalent to the other types, it seems preferable to separate them as distinct, just as is done with the Annelida and Mollusca, and the Annelida and Prosopygia.

Starting, then, with the supposition that *Peripatus* has descended from Annelid ancestors and represents the ancestors of the Myriapoda, the relationships of the various orders of this class and of the Insects remains to be traced. Unfortunately a large gap exists between *Peripatus* and any recent Myriapods, and it is possible that this class is a heterogeneous group; indeed by some recent authors it has been suggested that it should be done away with as a class, the Chilopods being united with the Insecta to form one class, while the Diplopods (perhaps with the Pauropoda associated with them) should form a second. There is no doubt but that *Peripatus* possesses many tracheate peculiarities, but its affinities to the remaining Tracheates are much more remote than those which exist between the various groups of Myriapoda, or between any of these groups and the Insecta. The character of the various appendages considered in relation with the nervous system seems to afford an admirable means of indicating the relationships of the various groups. The brain of Peripatus seems to be formed by the fusion of three pairs of ganglia; the most anterior and dorsal of these gives rise to the antennal nerve and the most posterior innervates the mandibles, while upon the middle one, which is closely related to the mandibular ganglion, the eye seems to be placed. It may be assumed that the ganglia with which the eyes are associated represent the Annelid supracœsophageal or cerebral ganglia and may therefore be termed the protocerebrum, while the antennary ganglia form the deutocerebrum, and the mandibular the tritocerebrum. In the Myriapods and Insects the brain is also composed of three parts to which the same names are applied, the antennæ being innervated from the deutocerebrum, while the tritocerebrum lacks a corresponding appendage, though in certain Insects transient indications of a tritocerebral appendage have been seen. Bearing these facts in mind, the ganglia and appendages of the various groups may thus be tabulated, and to make the comparison complete the Crustacea are also included.

Ganglion.	**Crustacea.**	**Peripatus.**	**Diplopoda.**	**Chilopoda.**	**Insecta.**
Deutocerebral.	…………………	Antennæ ?	Antennæ	Antennæ	Antennæ
Tritocerebral.	Antennules	Mandibles	…………	…………………	…………………
1st postoral	Antennæ	Oral papillæ	Mandibles	Mandibles	Mandibles
2d "	Mandibles	1st legs	Maxillæ	1s maxillæ	1st maxillæ
3d "	1st maxillæ	2d "	1st legs	2d "	2d "
4th "	2d "	3d "	2d "	Maxillipedes	1st legs
5th "	1st thoracic limb	4th "	3d "	1st legs	2d "
6th "	2d " "	5th "	4th "	3d "	3d "

It will be seen from this that in the Diplopoda the arrangement is intermediate between that found in *Peripatus* and that of the Chilopoda, while these latter approach closely the Insecta, and this seems to be the actual relationship, *Scolopendrella* forming an intermediate link between the Chilopods and the Insecta, approaching the Thysanura closely in the arrangement of the mouth-parts and in the number of segments of which the body is composed. The Diplopoda, it is true, pass through a larval stage in which but six legs are present, and it might at first sight be supposed that this indicates an affinity with the Insecta, but these legs do not belong to the same segments as do those of the Insects, and furthermore the occurrence of rudimentary abdominal appendages in some Thysanura, as well as in the embryonic stages of probably all Pterygota, indicates that the Insecta have been derived immediately from forms with many pairs of appendages, and these forms seem to be represented most accurately by the existing *Scolopendrella*.

SUBKINGDOM METAZOA.

TYPE TRACHEATA.

I. Class PROTRACHEATA.—Annelid-like forms; trunk not differentiated into thorax and abdomen; with nephridia. *Peripatus.*

II. Class MYRIAPODA.—Elongated forms; trunk not differentiated into thorax and abdomen; posterior trunk-segments with appendages in the adult.

1. Order *Pauropoda.*—Small forms; with only one pair of maxillæ; antennæ ending in three flagella; reproductive orifices at basis of third pair of trunk-appendages. *Pauropus*, *Eurypauropus.*
2. Order *Diplopoda.*—With only one pair of maxillæ; antennæ simple; reproductive orifice on second or between second and third trunk-segments; most of the trunk-segments with two pairs of legs. *Iulus*, *Lysiopetalum*, *Polydesmus*, *Strongylosoma*, *Glomeris.*
3. Order *Chilopoda.*—With two pairs of maxillæ and with maxillipeds; antennæ simple; reproductive orifice on the antepenultimate segment; each trunk-segment with a single pair of legs. *Geophilus*, *Scolopendra*, *Lithobius*, *Scutigera.*

4. Order *Symphyla.*—With only one pair of maxillæ and no maxillipeds; antennæ simple; most of the trunk-segments with a single pair of legs. *Scolopendrella.*

III. Class Insecta.—Trunk differentiated into thorax composed of three rings and an abdomen with typically ten segments.

1. Subclass *Apterygota.*—Thorax without wings; abdominal segments sometimes with rudimentary limbs in the adult.

1. Order *Thysanura.*—Abdomen with ten segments, bearing two or three cerci; abdominal appendages frequently present. *Lepisma*, *Campodea.*

2. Order *Collembola.*—Abdomen with six segments terminating in two springing-organs; abdominal appendages wanting. *Podura*, *Anurida.*

2. Subclass *Pterygota.*—With usually two pairs of wings situated on the meso- and metathoracic segments; abdominal appendages wanting in adults.

1. Order *Dermaptera.*—Abdomen with forceplike cerci; anterior wings small and chitinous, posterior folded like a fan and also transversely; mouth-parts biting; metamorphosis gradual. *Forficula*, *Labia.*

2. Order *Orthoptera.*—Abdomen usually with cerci; anterior wings chitinous, covering the posterior, which fold fanlike and sometimes also transversely; mouth-parts biting; metamorphosis gradual. *Caloptenus*, *Gryllus*, *Gryllotalpa*, *Periplaneta*, *Diapheromera.*

3. Order *Ephemeridæ.*—Abdomen with two long cerci; wings membranous and richly veined, the anterior larger; not folded when at rest; mouth-parts biting, but reduced; metamorphosis incomplete. *Ephemera.*

4. Order *Odonata.*—Abdomen with two platelike cerci; wings membranous and richly veined, not folded when at rest; mouth-parts biting; metamorphosis incomplete, sometimes approaching completeness. *Libellula*, *Æschna*, *Agrion*, *Diplax.*

5. Order *Plecoptera.*—Abdomen usually with cerci; wings membranous, moderately veined with few cross-veins; the anterior covering the posterior when at rest; mouth-parts biting; metamorphosis incomplete. *Perla.*

6. Order *Corrodentia.*—Abdomen without cerci; wings sometimes wanting (parasites and neuters), membranous, the anterior covering the posterior when at rest; mouth-parts biting; metamorphosis incomplete or wanting. *Termes* (with polymorphism), *Atropos*, *Liotheum*, *Trichodectes.*

7. Order *Thysanoptera.*—Abdomen without cerci; wings sometimes wanting, narrow, poorly veined, fringed with hairs; the anterior pair covering the posterior when at rest; mouth-parts piercing and sucking; metamorphosis incomplete. *Thrips*, *Phlœothrips.*

8. Order *Rhynchota.*—Abdomen without cerci; basal portion of anterior wings chitinous, posterior wings and tips of anterior membranous, or else both membranous, the anterior the larger, or both wanting; mouth-parts piercing and sucking; metamorphosis incomplete.

   Anterior wings chitinous at base (*Hemiptera*). *Anasa, Notonecta, Belostoma, Ranatra, Hydrometra, Halobates, Cimex, Pediculus* (wings wanting in the last two).

   Anterior wings both membranous (*Homoptera*). *Cicada, Aspidiotus, Dactylopius, Pemphigus, Aphis* (wings may be wanting in the last three).

9. Order *Coleoptera.*—Abdomen without cerci; anterior wings chitinous, covering in the posterior when at rest; mouth-parts biting; metamorphosis complete.

   (*a*) Tarsi of four joints, one of them very small (*Cryptotetramera*). *Coccinella.*

   (*b*) Tarsi of five joints, one of which is very small (*Cryptopentamera*). Curculionidæ, *Clytus, Saperda, Monohammus, Doryphora.*

   (*c*) Tarsi of posterior legs four-jointed, of two anterior pairs five-jointed (*Heteromera*). *Meloë, Lytta.*

   (*d*) Tarsi all five-jointed and all the joints of equal size (*Pentamera*). *Lampyris*, Elateridæ, *Melolontha, Necrophorus*, Staphylinidæ, *Hydrophilus, Gyrinus, Brachinus, Harpalus, Carabus, Calosoma, Cicindela.*

10. Order *Neuroptera.*—Abdomen without cerci; wings membranous, richly veined with numerous cross-veins; mouth-parts biting; metamorphosis complete. *Corydalis, Chrysopa, Myrmeleon.*

11. Order *Panorpata.*—Abdomen sometimes with cerci; wings membranous with few cross-veins; mouth-parts biting, at end of cylindrical rostrum; metamorphosis complete. *Panorpa.*

12. Order *Trichoptera.*—Abdomen without cerci; wings covered with hairs or scales, posterior ones larger and folded fanlike when at rest; mouth-parts sucking; metamorphosis complete. *Phryganea, Anabolia.*

13. Order *Lepidoptera.*—Abdomen without cerci; wings covered with scales, not folded when at rest, though they may overlap; mouth-parts usually sucking; metamorphosis complete.

    Small forms (*Microlepidoptera*). *Tinea, Carpocapsa*, Pyralidæ.

    Larger forms (*Macrolepidoptera*). Geometridæ, *Clisiocampa, Orgyia, Telea, Pieris, Vanessa, Papilio.*

14. Order *Hymenoptera.*—Abdomen without cerci; wings membranous, without scales, not folded; mouth-parts biting and lapping; metamorphosis complete.

    Ovipositor retractile with poison-gland (*Aculeata*). *Apis, Bombus, Vespa, Camponotus, Formica.*

Ovipositor non-retractile, without poison-gland (*Terebrantia*). *Ichneumon*, *Proctotrupes*, *Pteromalus*, *Microgaster*, *Cynips*, *Selandria*.

15. Order *Diptera*.—Abdomen without cerci; wings sometimes wanting, only the anterior pair ever present, posterior pair represented by halteres; mouth-parts piercing and sucking; metamorphosis complete.

With wings. *Culex*, *Tabanus*, *Musca*.

Without wings. *Pulex*, *Melophagus*.

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CHAPTER XVI.

TYPE ECHINODERMA.

THE Echinoderms are exclusively marine organisms and vary considerably in shape, some forms being elongated and vermiform, others stellate, and others again almost spherical. Whatever may be the shape, however, a well-marked radial symmetry can be distinguished, which suggested to the older zoologists the association of the members of this group with the Cœlentera in a type Radiata. The radii in the Echinoderma are, however, almost invariably five, instead of four or six or some multiple of these numbers as in the Cœlentera; and, furthermore, while in the Cœlentera the radial symmetry represents a primitive condition and any departure from it towards bilaterality, as in the Anthozoa, is secondary, the reverse is the case with the Echinoderma. The larval forms of this group are strictly bilateral, and even in the adults certain organs or parts of organs interfere with the regularity of the pentamerous arrangement and bring about a more or less pronounced bilaterality.

This may be clearly seen if one of the stellate forms, such for instance as the ordinary five-rayed Starfish (Fig. 246), be examined. This animal consists of a central disk, at the centre of one surface of which, the oral surface, the mouth is found, while the anus occupies a somewhat excentric position on the other surface, which may be termed the aboral or apical surface. From the edge of the disk the five arms or rays project outwards, and along the median line of the oral surface of each arm there extend outwards from rings around the mouth a nerve-cord and a hydrocœl canal, this latter forming a part of a peculiar system of vessels characteristic of the Echinoderms. In consequence of this radiation of these structures out along the arms, and the arrangement of the other organs for the most part in conformity with the radiation, the arms may be regarded as representing the radial axes of the body, the interradial axes lying in the intervals between them. If now the aboral surface of the disk be examined, there will be found upon it, in one of the interradii, a peculiar tubercle, known as the madreporiform tubercle, which serves to place the hydrocœl system of canals in communication with the exterior water. There is but one such tubercle, and but one canal leading down from it to the hydrocœl ring which surrounds the mouth, and consequently there can be but one plane in which the animal can be divided into two similar parts. Therefore the Starfish, though superficially appearing to possess a radial symmetry, is fundamentally bilateral—a statement which applies equally well to any member of the Echinoderm type.

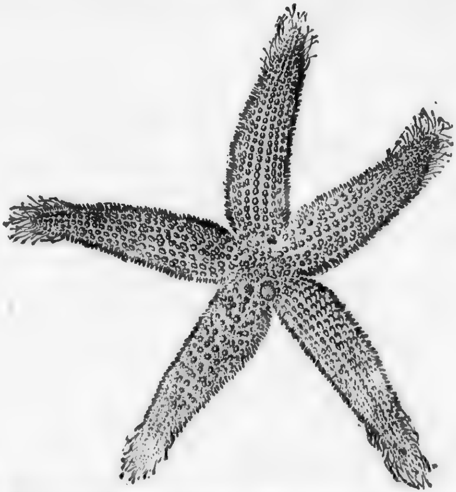


FIG. 246.—*Asterias arenicola* (after AGASSIZ from VERRILL).

It does not necessarily follow, however, that the plane which passes through the madreporiform tubercle is the median plane of the body. The larvæ of the Echinoderms are strictly bilateral organisms, no sign of radiality being found in them in an early stage of development, and it would seem more satisfactory to take as the median plane of the adult animal one which corresponds as closely as possible with the larval median plane. The madreporiform tubercle, or rather the pore which corresponds to it, and the tube which leads from it to the rudiment of the hydrocœl system can readily be made out in the larvæ of most forms, and it can be seen that it lies to the left of the median plane of the body. Indeed in the larvæ of some Starfishes two pores occur at an early stage of development, one to the left and the other to the right of the median plane, the latter subsequently disappearing. The madreporiform tubercle might therefore be regarded as lying to the left of the median plane, which will accordingly pass through the radius to the right of the tubercle.

However, it is impossible to tell how much modification has taken place during the transition from the bilateral to the radial condition, and it is not impossible that the greater portion of the adult represents one of the halves of the embryo, the other half remaining more or less undeveloped. Furthermore a secondary bilaterality supervenes in certain forms of Echinoidea and Holothuroidea which does not agree with that indicated in the preceding paragraph, and is not indeed the same in the two groups. It seems therefore preferable to assume a perfectly arbitrary method of indicating the radii of the body, calling that radius which lies opposite the madreporiform tubercle *A*, that which lies to the left of this when the animal is held with the oral surface upwards *B*, and so on *C*, *D*, *E*, following the direction of the hands of a watch. The interradii may be indicated by combining the letters of adjacent radii, the interradius between *A* and *B* being denoted by *AB*.

The body-wall in the Echinoderma is covered on the outside by a usually delicate, and in some cases ciliated, ectoderm, which may, however, be indistinguishable from the subjacent mesodermal tissues in certain parts of the body. Below this ectoderm, when present, comes a layer of mesodermal connective tissue consisting of relatively few cells imbedded in a more or less fibrillar matrix, and in this connective tissue there are imbedded numerous calcareous plates, in some forms, such as the Holothurians, somewhat widely separated from one another so that the body-wall has a more or less leathery consistency, but more frequently placed almost or quite in contact with each other, and uniting in most of the Echinoids or Sea-urchins to form a firm test enclosing the principal vegetative organs, a small area or peristome around the mouth alone remaining but partially calcified and retaining a leathery consistency. Spinous elevations are frequently developed upon these dermal plates (whence the name of the type) and may assume various forms, being in some cases quite long, movably articulated with the plates, and supplied with muscles so that they may aid in locomotion.

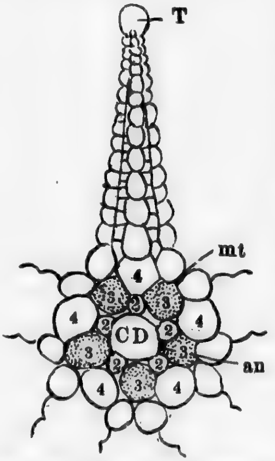


Fig. 247.—Disk and Arm of *Zoroaster*, showing the Apical System of Plates (after Sladen).

an = anus.
cd = centro-dorsal.
mt = madreporite.
T = terminal plate.
2 = under-basals.
3 = basals.
4 = radials.

The arrangement of the calcareous plates differs greatly in the different classes which compose the type, but certain of them, distinguishable by their position and relative arrangement, reappear in the majority of the classes. These plates are situated at the oral and aboral surfaces of the body. The oral plates are not so constant nor so numerous as the aboral or apical, and show a tendency, even in those groups in which they are most highly developed, to undergo a greater or less amount of resorption during development, being frequently more pronounced in larval than in adult life. Typically the oral system consists of a central oral plate, the *orocentral*, unknown in recent forms, but occurring in certain fossil genera, and this is surrounded by a ring of five plates, which may be termed the oral plates, and which have an interradial position. The apical system has as a central plate the so-called *centro-dorsal* (Fig. 247, *CD*), which in some forms is replaced by a number of small plates between which the anal opening of the digestive tract is to be found. Forming a ring around this are frequently five plates possessing a radial position which are termed the *under-basals* (Fig. 247, 2) and are unrepresented in certain forms; next to these comes a second circle of five plates, the *basals* (Fig. 247, 3), which are interradial and correspond to the oral plates, while next to these again is a third cycle, also of five plates, the *radials* (Fig. 247, 4), whose name denotes their position. Numerous other plates may intervene in the various groups between the radials and the orals, but their number and arrangement is not sufficiently constant to permit of homologies; the oral and apical systems are, however, represented more or less perfectly in all but one of the classes, and consequently deserve special mention.

A well-developed dermal muscular system occurs in the Holothurians in which the calcareous plates are scattered and the body-wall consequently capable of considerable contraction and expansion, but in other forms it is very much reduced. In those forms in which the calcareous plates are simply in apposition strands of muscular tissue pass from plate to plate, a considerable amount of movement being possible, but in the Sea-urchins, for example, the dermal musculature is almost wanting, being reduced to bands passing to the bases of the movable spines and to the complicated masticatory apparatus.

The cœlom is somewhat complicated in its relations, which vary considerably in the different groups. In all enterocœlic and schizocœlic portions are distinguishable, the former in the embryo arising as pouchlike diverticula from the primitive intestine or enteron, and later becoming completely constricted off from it. Much variation occurs in the later history of the pouches in the various groups, but in general it may be stated that one of them, the left, has a portion constricted off from it, which forms the adult *water vascular system* or *hydrocœl*, a structure characteristic of the Echinoderms; and furthermore this same left enterocœl communicates with the exterior by a dorsal pore, situated in the interradius *CD*, and represented in the adult by one or many pores opening upon a sievelike calcareous plate known as the *madreporiform tubercle* or *madreporite.* The hydrocœl in the adult communicates with the left enterocœl by a tube, termed the *stone-canal* from the deposition of calcareous matter which occasionally takes place in its walls, and so indirectly opens to the exterior through the madreporiform tubercle (see Fig. 265). The various departures from this arrangement which occur will be more conveniently considered in connection with the special descriptions of the various groups; the condition just mentioned may be provisionally accepted as representing the typical arrangement.

After the separation of the hydrocœl from the left enterocœl, the latter and the enterocœl of the right side increase in size and finally apply themselves closely to the inner surface of the body-wall and to the outer surface of the digestive tract, forming the peritoneal lining of these structures. Where the two cœlomic sacs meet there are formed, of course, two partitions extending from the body-wall to the intestine, and suspending that structure between them. These partitions are the mesenteries, but before the embryo reaches the adult stage one of these mesenteries disappears, the other persisting in a more or less perfect form. The coiling of the intestine, which occurs frequently in the adult forms, brings about complications of the course of the mesentery, complications further increased in most cases by the formation of other partitions which may traverse a greater or less portion of the cœlom either longitudinally or transversely. One of the transverse partitions, most frequently present, separates off more or less completely from the rest of the cœlom, a portion of it surrounding the pharyngeal region of the digestive tract and hence termed the peripharyngeal cavity, while in some cases a perianal cavity may similarly be formed.

The hydrocœl, whose origin has been described, develops into a tubular ring (Fig. 248, *cc*) surrounding the œsophagus quite close to the mouth. Upon this ring in the interradii one or several saclike diverticula, termed *Polian vesicles* (*p*), occur, and in one interradius a canal, the stone-canal (*sc*), passes aborally to open into a thin-walled sac termed the *ampulla of the stone-canal*, which is in reality a portion of the left enterocœl, partly or wholly separated off from the rest of that cavity. This ampulla, as already mentioned, communicates with the exterior through the madreporite. In the radii tubes (*rc*) arise from the ring which extend out to the aboral extremity of the body in the elongated and spherical forms, and to the ends of the rays in the brachiate forms, terminating frequently in tentacular structures (*t*) which protrude to the exterior, pushing the ectoderm before them. Along the course of these tubes lateral branches are given off which terminate either in tentacular structures, or else in tubes terminating in a sucker, which, since they play an important rôle in locomotion, are termed *tube-feet* (*tf*). In many forms a globular reservoir or *ampulla* (*a*) is attached to each tube-foot, and valves are found at the junction of the branch passing to the foot with the radial canal, so that the foot can be extended to a considerable distance by the contraction of the muscles in the walls of the ampulla and the consequent forcing of water into it. By means of the sucker they may then adhere to foreign objects, and their contraction then produces a movement of the body towards the point of fixation.

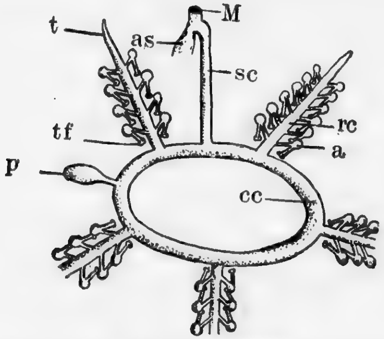


FIG. 248.—DIAGRAM TO SHOW THE ARRANGEMENT OF THE HYDROCŒL OF AN ECHINODERM.

a = ampulla.
as = axial sinus.
cc = circular canal.
M = madreporite.
p = Polian vesicle.
rc = radial canal.
sc = stone-canal.
t = terminal tentacle.
tf = tube-foot.

In connection with the stone-canal a peculiar body is developed in most forms. Its function is a matter of question, it having been at one time taken for the heart and at another for a gland. It is generally termed the ovoid gland (Fig. 265, *og*) and consists of a mass of cells, derived from the peritoneal lining of the enterocœl, grouped together to form a more or less solid mass. The oral end of the gland is prolonged into a cordlike structure which seems to enter into close relationships with the oral lacunar ring (see below), while at the other it is continued out to enter into close relationships with the reproductive organs in a manner that will be described when treating of those organs. Surrounding the gland is a sinus—the axial sinus (Fig. 265, *as*)—separated off from the enterocœl and, in some forms, in communication with the ampulla of the stone-canal, and the portion of the gland which passes off towards the reproductive gland is also surrounded by a sinus, or rather lies in the wall of a sinus which may or may not communicate with the axial sinus but has, like it, origin from the general enterocœl.

What has been termed a blood system is usually present, consisting of a tubular ring surrounding the œsophagus, and lying between the hydrocœl-ring and the nerve-ring. Five branches may extend off from it along the radii, preserving the same relations to adjacent structures as does the ring. These spaces seem to be schizocœlic in their character, and may be termed the *schizocœlic ring* and *radial schizocœlic sinuses* in order to avoid confusion with another system of vessels which sometimes lie within the sinuses and have also been termed blood-vessels. This latter system may be termed the *lacunar system*, and is composed of a network of vessels lying in the walls of the intestine, and collecting usually into a periœsophageal ring or plexus (Fig. 265, *lr*), with which also the ovoid gland comes into connection. In the Echinoids, as has just been indicated, prolongations of this periœsophageal ring or plexus extend out in the radial schizocœlic sinuses.

The fluids contained in the sinuses, lacunæ, hydrocœl, and enterocœl are all very similar, consisting of a plasma containing amœboid cells sometimes deeply pigmented. In a few forms hæmoglobin is present; in the Ophiuran *Ophiactis* it is contained in flat non-nucleated disks, resembling Mammalian red blood-corpuscles, floating in the plasma of the water vascular system; in the Holothurians, *Thyone* and *Cucumaria*, it is, however, contained in amœboid corpuscles, which are most abundant in the cœlomic fluid, though occurring also in the water vascular tubes.

The digestive tract is generally more or less twisted into a spiral; and even when, as in some Holothurians, it appears to be straight, it is to be regarded as a much-drawn-out spiral, since the mesentery still retains a spiral arrangement. In the Holothurians, Echinoids, and Starfishes it opens on the aboral surface of the body, but in the Crinoids it is bent upon itself so that the anus is on the oral surface. In some Starfishes and in all Ophiurans no anus is present. Various accessory structures, masticatory apparatus, cœcal pouches, etc., are found in the various groups, but their description may be deferred until later.

The nervous system may be regarded as being composed of three portions, one of which has essentially the same arrangement as the water vascular tubes, consisting of a circumoral or a periœsophageal ring from which five radial nerves pass off (Fig. 265, *nr* and *rn*). In the Starfishes and Crinoids the entire system is imbedded in the ectoderm, but in other forms it sinks within the body-cavity. From it branches pass inwards at the mouth to supply the walls of the œsophagus, and other branches form a network covering the surface of the body, supplying the sense-organs which may occur thereon. The radial nerves, in addition to sending branches to join the epidermal plexus, supply the ambulacral system. This portion of the nervous system may be termed the epidermal portion, and the second, inasmuch as it supplies the majority of the muscles of the body, may be termed the muscular system. This is not always developed, being absent in the Crinoids, but when present accompanies in general the epidermal portion in the form of delicate nerve-cords lying on the inner surface of the circumoral ring and radial nerves, and sending branches to the various muscles, including possibly those of the tube-feet. The third or aboral portion appears to be entirely wanting in the Holothurians, but when present consists of a ring situated at the aboral surface of the body, sending off branches to the reproductive organs as well as, in some cases at least, forming anastomoses with the epidermal system.

Sense-organs of various kinds are developed. Tactile tentacles occur at the extremities of the radii of some forms and round the mouth in others, while in the softer-skinned Holothurians tactile papillæ may occur. Eyes occur at the extremities of the radial nerves of the Starfishes, and have also been described as occurring in some Echinoids, while otocysts occur in some Holothurians, sometimes in considerable numbers.

No special excretory organs occur in the Echinodermata, the amœboid cells of the cœlomic fluids perhaps serving in some cases to remove the waste substances. They have been observed to pass through the body-wall, in regions where it is thin, to the exterior and there degenerate. For the most part, however, the waste products are deposited in the tissues, or else pass to the exterior by osmosis. In the Holothurians special branched appendages of the terminal portion of the intestine appear to take some part in excretion, but such organs do not occur in other groups.

The Echinoderms are almost invariably bisexual, and the reproductive organs are usually situated in the interradii. They are enclosed in a special cœlomic sinus, the *genital sinus*, in whose wall may be found the branches of the aboral nerves. From each organ or mass of reproductive cells a cellular cord, the *genital rachis*, surrounded by the sinus may be traced, except in the Holothurians, to the ovoid gland, and it appears probable that in some cases at least the reproductive cells originate in a part of the ovoid gland and migrate to the reproductive organ along the rachis, becoming mature in their final position. The openings by which the reproductive elements pass to the exterior vary both in number and position in the different groups, but are usually situated on the aboral surface of the body.

I. CLASS **CRINOIDEA.**

The Crinoids, or Sea-lilies (Fig. 249), constitute a group of forms which in the earlier geological periods reached a high grade of development, but to-day the class is represented by comparatively few forms, for the most part confined to deep water. One of the most characteristic features of the group is the presence of a more or less elongated cylindrical stalk, one end of which is attached to stones or other objects which serve as supports for the animal, while at the other end is the body proper, which has a more or less cuplike form. In the peculiar genus *Holopus* the stalk is thick and short, and may be described rather as the prolonged apex of the body

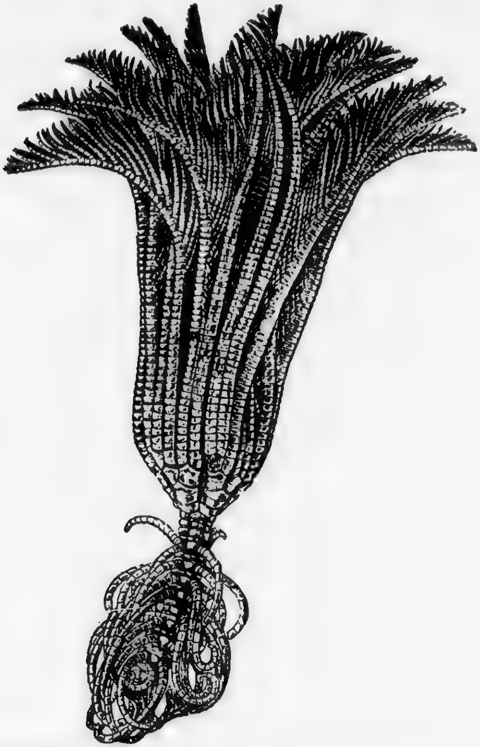


FIG. 249.—*Pentacrinus maclearanus* (after WYVILLE THOMPSON from HERTWIG).

than as a distinct stalk, while in other forms, such as *Antedon* and *Actinometra*, the stalk, though present in young forms, is entirely wanting in adult life, during which the animal is free-swimming, though having the power of anchoring itself temporarily to solid objects by means of a number of slender processes termed *cirri* which project from the apex of the cup (Fig. 251, *c*).

The lower portion of the cup, or *calyx*, is formed by a number of series of calcareous plates united to each other by sutures, while its mouth is covered in by a flat or dome-shaped disk in which calcareous plates may or may not be present. In the centre of the disk is the mouth of the animal, while to one side is the anus, lying in the interradius *CD*. From the mouth five grooves, known as the *ambulacral grooves*, extend outwards towards the margin of the cup, and, near the margin, branch, being then continued outwards on the oral surfaces of ten arms which arise from the junction of the disk and calyx, frequently branching in their course, and bearing along their sides a series of short processes resembling them in structure, and termed the *pinnules*, upon which the ambulacral grooves are also continued. These arms are capable of considerable movement, being at one time extended out at right angles to the body or even reflexed, and at another coiled up circinnately over the disk, the pinnules being at the same time bent inwards towards the median axis of the arm.

The stem when present consists of a number of disklike or cylindrical calcareous plates, placed one on top of the other, being held together by bands of connective tissue, and is traversed by a central canal containing prolongations of certain of the visceral structures. The terminal plate serves as the point of fixation, the plates immediately above it having attached to them a number of *cirri* which assist in fixation and are, like the stem, composed of calcareous plates containing prolongations of the central canal. In some forms, such as *Pentacrinus*, whorls of cirri also occur at intervals all along the stem, those plates from which they arise being termed nodal plates, a varying number of plates destitute of cirri occurring between two nodes in different genera. In certain genera, however, such as *Hyocrinus* and *Rhizocrinus*, these stem cirri are entirely wanting except near the point of fixation.

The uppermost plate of the stem is usually regarded as forming the apex of the calyx and is termed the *centrodorsal.* Above this comes in most recent forms a series of usually five (sometimes three) interradial plates, the basals (Fig. 250, *b*), but in one genus, *Thaumatocrinus*, there occurs between the centrodorsal and basal plates a series of five radial plates which are termed the parabasals or underbasals, and which have also been found to occur in the embryo of *Antedon*, later on fusing with the centrodorsal. Succeeding the basals are from two to seven circles of radials (*r*), each circle being also composed of five plates termed the first, second, third, etc., radials according to their succession counting from the centrodorsal. In *Antedon* and some of its allies the number of cycles of radials seen from the exterior is one short of the actual number which exists, the first radials being overlapped and covered in by the second; and furthermore in the same forms the basals have also been pushed, as it were, within the calyx and have fused to form a single plate, the so-called *rosette plate* (Fig. 251, *Ros*), which rests upon the centrodorsal, partially closing a cavity in that plate. The terminal radials usually present two articulating facets in their distal surfaces and are generally known as the *axillaries* (Fig. 250, *a*), since the arms articulate with them. In the genus *Thaumatocrinus* between each pair of first radials an interradial plate occurs, a condition frequently found in fossil genera (*i*), but usually wanting in recent forms. These various plates which constitute the apical system are united by sutures, the edges of the various series of plates coming into contact, so that a firm support is afforded for the arms.

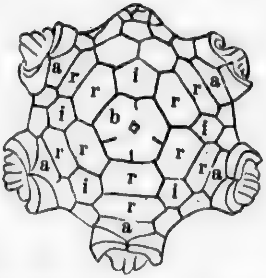


FIG. 250.—THE APICAL SYSTEM OF *Melocrinus* (FOSSIL) (from BRONN).

a = axillary plates.
b = basal plates.
i = interradial plates.
r = radial plates.

These are in reality continuations of the radial series of plates; in fact, in some forms certain of the radials appear to enter into the formation of the arm. In most forms, however, a series of arm-plates arises from each facet of the five axillary plates, so that the arms are ten in number—a condition which finds an exception in the remarkable genus *Thaumatocrinus*, which possesses but five. In some forms these ten arms branch dichotomously; the plates intervening between the axillaries and the first branching are termed *brachials*, those between the first and second branchings *distichals*, and those between the second and third branchings *palmars*—terms which are useful in systematic descriptions. These various plates are united together by ligaments and muscles, or else by ligaments alone (this last form of union being known as a *syzygy*), the movements of the arms noted above being thus rendered possible. The pinnules repeat the arm in their structure, though usually on a much-reduced scale. They are situated on the joints separating consecutive plates of the arms, and are placed alternately on the right and left sides of the arm which bears them. They appear at first to have been produced by lateral budding from the joints, but closer examination indicates that in reality they represent a branching, one of the branches remaining small, while the other increases in size and places itself in the direction of the axis of the arm. The whole arrangement is comparable to that form of inflorescence termed by botanists a scorpioid cyme, the pinnules representing the flower-pedicels. Owing to the pinnules being in reality one of the branches of a dichotomy, it is evident why, in those forms in which the arms branch, there is no pinnule at the joint where the branching occurs; in addition, however, pinnules are also lacking on syzygial joints, so that their regular succession may be somewhat disturbed.

As regards the oral system of plates an *oro-central* is found in some fossil forms, but is unrepresented in recent genera. A circle of five interradial oral plates is found in *Holopus*, *Rhizocrinus*, *Hyocrinus*, *Thaumatocrinus*, and *Calamocrinus*, and in the stalked larva of *Antedon*, but in the adults of this latter form and in other genera than those mentioned these plates disappear during growth, the disk being either naked, or covered by a number of small plates which are termed *anambulacrals*, certain of which lying on either side of the ambulacral grooves receive the special name of *adambulacrals*, or covering-plates.

The ectoderm cannot usually be distinguished over the surface of the calyx or on the stem, but is present on the disk and on the oral surfaces of the arms and pinnules, being there non-ciliated except along the ambulacral grooves. It rests upon a connective tissue in which the calcareous plates are developed, and from which strands, frequently with calcareous spicules imbedded in them, usually traverse the body-cavity. The ligaments which unite the plates of the arms and stem are formed of this connective tissue, and contractile fibres of a peculiar character are sparingly developed in it, stretching across the non-syzygial joints of the arms, pinnules, and cirri, and probably also reaching a slight development in the stem.

The internal structure of the Crinoids is known principally from observations on *Antedon*, and the following account represents what occurs in that form. The cœlom, as already stated, is traversed by numerous strands of connective tissue, and primarily consists of two cavities separated from each other by a mesentery, each cavity being continued out into the arms, forming the oral and aboral canals of these structures, at the extremities of which they unite. The mesentery does not, however, long persist in its entirety, but the two cavities fuse, new membranes, however, arising and dividing them in some species of *Antedon*. One of these membranes (Fig. 251, *vs*) surrounds the intestine and forms the visceral sac, its presence rendering the evisceration of *Antedon* an easily-accomplished process and one which is made use of by the animal in unfavorable conditions, a new visceral mass being later regenerated. The portion of the cœlom which lies peripherally to this sac is termed the circumvisceral portion (*cc*), and that within it the intervisceral (*ic*), the latter containing an axial cavity (*Ax*) enclosed by a membrane similar to the visceral sac and continuous with the oral cœlomic cavities (*oc*) of the arms, the aboral cavities (*ac*) communicating with the circumvisceral cœlom. A portion of one of the cœlomic cavities at an early stage becomes cut off from the rest of the cœlom and divided into five chambers whose walls are formed of a dense fibrous membrane. This constitutes

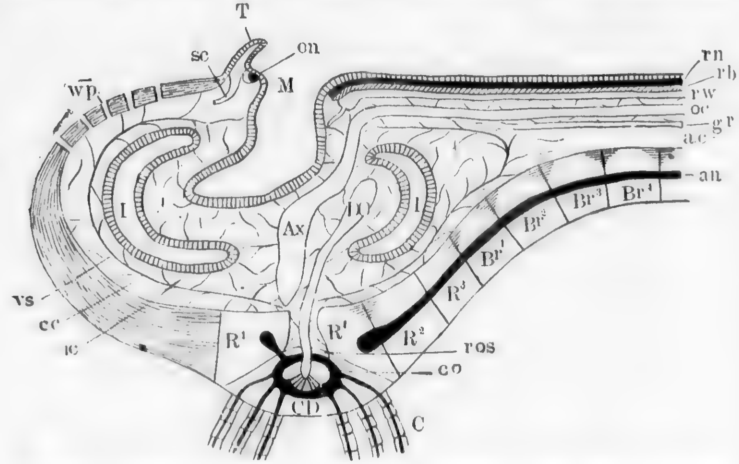


FIG. 251.—VERTICAL SECTION THROUGH *Antedon* (combination of figures by LUDWIG and MARSHALL).

ac = aboral canal of arm.
an = aboral nerve.
Ax = axial sinus.
Br = brachial plates.
C = cirri.
cc = circumvisceral cavity.
CD = centrodorsal plate.
co = central organ.
Do = dorsal organ.
gr = genital rachis.
I = intestine.
ic = intervisceral cavity.
M = mouth.
oc = oral cavity of arm.
on = oral nerve-ring.
R = radial plates.
rb = radial lacunar vessel.
rn = radial epithelial nerve.
ros = rosette-plate.
rw = radial hydrocœl-canal.
sc = stone-canal.
T = oral tentacle.
vs = visceral septum.
wp = water-pore.

the chambered organ (*co*), which in *Antedon* lies in a cavity in the centrodorsal plate and is roofed over by the rosette-plate, but in other forms simply rests upon the centrodorsal; communicating with it is the lower end of a somewhat club-shaped structure termed the *dorsal organ* (*Do*), which projects orally parallel to the axial cœlomic cavity.

The epithelium of the aboral cœlomic cavities of the arms is differentiated here and there into peculiar organs the ciliated cups, consisting of slight depressions lined by columnar cells each of which bears a long cilium. These cups are especially abundant in the pinnules, and serve to create a circulation of the cœlomic fluid, which, as in other Echinoderms, contains numerous amœboid cells floating freely in it.

The water vascular system, or hydrocœl, consists of a ring surrounding the mouth, and sending outwards five radial canals (*rw*) which lie below the ambulacral grooves and are continued along the arms and pinnules. Occasionally subambulacral calcareous plates are developed in the connective tissue below the radial canals, and in some fossil forms these plates assume a regular arrangement in two rows. At regular intervals along the arms are situated the ambulacral tentacles, which are fingerlike outpouchings of the radial canals destitute of terminal suckers and are arranged in groups of three, the canals being somewhat enlarged in the region where they occur, an indication perhaps of the ampullæ found in other groups; in some forms the cavities of the tentacles seem to be united with those of the canals only by exceedingly small orifices, which may be closed, since the tentacles in their greatest contraction always remain filled with fluid. In the neighborhood of the mouth are a number of oral tentacles (Fig. 251, *T*) arising directly from the oral ring, and differing from the ambulacral tentacles in not being arranged in groups of three. From the oral ring there also arise in *Antedon* a number of ciliated tubes (*sc*) which open into the cœlomic cavity, each one corresponding to a stone-canal of the other Echinoderms. In *Antedon* there are as many as thirty of these canals in each interradius, and in *Pentacrinus* an even greater number occurs; but in other forms they may be fewer, *Rhizocrinus*, for example, possessing only five in all, one being situated in each interradius. In the larva of *Antedon* there is at an early stage only one, communicating with a portion of one of the primary cœlomic cavities, which on its part opens to the exterior by a pore, an arrangement which may be regarded as typical for the Echinoderms. Later, however, this portion of the cœlomic cavity degenerates, and the canal then opens directly into the general cœlom, and this communicates with the exterior by the pore. In subsequent stages additional stone-canals develop from the oral ring, and at the same time additional pores develop in the walls of the body, forming what are called the *calyx-pores* (*wp*). These may reach a considerable number, it being estimated that in *Antedon* there are no less than fifteen hundred of them scattered over the disk; in *Rhizocrinus*, *Hyocrinus*, and *Holopus*, however, there are only five pores, one piercing each of the oral plates present in these forms.

The schizocœlic system consists of five radial sinuses (Fig. 251, *rb*) lying between the radial hydrocœl vessels and the more superficial radial nerve, together with, according to some authors, a circular sinus surrounding the mouth into which the radial sinuses open. A plexus of lacunæ occurs in the walls of the intestine, and another surrounds the œsophagus, this latter in part aggregating itself into a structure resembling a lymphatic gland and known as the spongy body; the dorsal organ likewise contains a dense network of tubes lined with epithelium. Along the sides of the hydrocœl-canals, in the disk, arms, and pinnules, alternating in the two last with the triads of tentacles, in the walls of the intestine, and occasionally elsewhere, there are imbedded in the connective tissue yellowish spherical bodies known as the *sacculi*. The interior of each sacculus is lined with cells, and contains a number of pyriform masses formed of small highly-refractive spherules, apparently of an albuminoid substance. The function of these bodies is very obscure; they have been regarded as organs for secreting carbonate of lime, as excretory organs, as parasites, as mucous glands, and lately as organs of reserve in which proteid matter may be stored up for future use. At present, however, the question is an open one, and a function cannot with certainty be assigned to them.

The mouth (Fig. 251, *m*) is usually situated at the centre of the oral disk, and opens into a simple tubular intestine which coils once round the cœlomic cavity in the direction of the hands of a watch and then, bending upon itself, turns orally to open in the interradius *CD* upon the disk. In *Actinometra*, a genus closely related to *Antedon*, the intestine lies in four coils, but there is as a rule little variation from the condition described, and no specially-marked differentiation of the tube occurs.

The nervous system of the Crinoids is characterized by the remarkable development of the aboral portion and by the apparently entire absence of the muscular portion. The epithelial portion consists of a ring and five radial nerves (*rn*) which pass along the ambulacral grooves and out upon the arms and pinnules, imbedded throughout their entire course in the lower layers of the ectoderm. The aboral system is, on the other hand, much more strongly developed, and stands in intimate association with the chambered organ in the walls of which it is imbedded. Its central portion is somewhat complex, as is shown in Fig. 252, but may be said to consist of a ring, or, more properly speaking, of a pentagon from which five strong cords radiate out into the arms, perforating the plates of which these are composed. Both fibres and ganglion-cells enter into the composition of the cords and ring, and a complicated system of commissures exists. From the central portion branches are also sent to the cirri, and probably in stalked forms a branch traverses the central cavity of the stalk, accompanying prolongations of the cavities

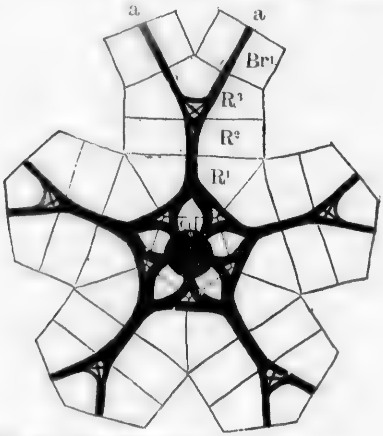


FIG. 252.—DIAGRAM OF THE ARRANGEMENT OF THE ABORAL NERVOUS SYSTEM OF *Antedon* (after MARSHALL).

a = arms.
cd = centrodorsal.
Br = brachial plates.
R = radials.

of the chambered organ. The terminal branches of the radial aboral nerves pass to the integument of the oral surfaces of the arms and to the muscles which unite the various plates, so that the system governs and coördinates the movements of the arms and pinnules as well as of the cirri. The epithelial system, on the other hand, controls the movements of the ambulacral and oral tentacles, stimulation of it causing movement of these structures in the immediate vicinity of the region to which the stimulus is applied.

Another system of nerve-fibres, consisting of a periœsophageal ring which sends off two branches to each arm, one lying on each side of each of the ambulacral grooves, and which is connected with nerve-fibres passing from the dorsal organ, has been described as occurring, but its significance has not yet been satisfactorily determined. No special sense-organs occur in the Crinoids.

The reproductive organs are developed for the most part in the pinnules, occasionally a slight development of them appearing in the arms or even in the body proper; in *Holopus* alone they are confined to the arms. They consist of tubes lined with germinal epithelium on their inner surfaces and enclosed within a prolongation of the cœlom. They lie between the two cœlomic prolongations of the arms already mentioned, and though the reproductive organs are developed only in the pinnules as a rule, nevertheless each genital tube or rachis (Fig. 251, *gr*) can be traced through the arm to the body, where it terminates in connection with the dorsal organ. In their development indeed they grow out from this organ, and it seems probable that the ova and spermatozoa mother-cells migrate out from it along the rachides to reach maturity in the pinnules. Comparing this with the condition in other Echinoderma, it seems clear that the so-called dorsal organ of the Crinoids is homologous with the ovoid gland of the other forms. The reproductive elements pass to the exterior by one or two ducts connected with each reproductive mass; the origin of these ducts is unknown.

The Crinoids seem to have been closely related to two groups of forms known only as fossils. These were the *Cystoids*, which appear in the Lower Silurian rocks and die out in the Carboniferous, and the *Blastoids*, which appear in the Upper Silurian and also disappear in the Carboniferous. For a description of these forms reference must be made to the standard works on Palæontology. On account of their similarity to the Crinoids they have been associated with them in the class *Pelmatozoa*, of which each of the groups formed an order; inasmuch, however, as the present work is concerned only with recent forms, it has been thought more convenient to regard the Crinoids as a class.

The class Crinoidea has been divided into two orders. The *Palæocrinida*, chiefly Palæozoic forms, characterized principally by the presence of under-basals and of a series of plates covering in the disk almost completely, to which may be added the usual presence of interradials and the greater width of one of the interradii, that in which the anus occurred (see Fig. 250). The *Neocrinida*, on the other hand, included the recent forms, the group making its first appearance in the Mesozoic, and is characterized by the disk being only imperfectly covered by plates, by the under-basals and interradials being absent, and the interradii all equal in width. Transition forms between the two groups occur, however, the genera *Hyocrinus* and *Calamocrinus*, for example, presenting certain Palæocrinid peculiarities combined with Neocrinid ones, and it seems more satisfactory to divide the class into families only, leaving orders out of the question.

Development of the Crinoids.—*Antedon* is the only Crinoid whose development has been studied. The embryo leads for a time a free-swimming existence, and possesses a somewhat ovoidal form (Fig. 253) with a tuft of cilia at the smaller anterior end and five rings of cilia surrounding the body. Not far from the anterior end is a slight groove, and lower down upon the side is a much larger one. This larva settles down upon the anterior end, the slight depression near this end serving as an organ of fixation, and then a rather remarkable rotation occurs, the large groove shifting round together with the interior organs until it comes to lie at the free end of the organism, and at the same time its lips unite so as to enclose a cavity, the vestibule. Calcareous plates have ere this developed in the connective tissue of the embryo and outline a stalked Crinoid into which the larva is gradually transformed, the larval skin shrinking as it were, so as to closely surround the stalk and calyx, while the vestibule opens to the exterior by the gradual thinning and final disappearance of its roof, its floor forming the ectoderm of the disk. After continuing its growth for some time as a stalked Crinoid, the young *Antedon* finally separates from its stalk, and thereafter leads a free existence.

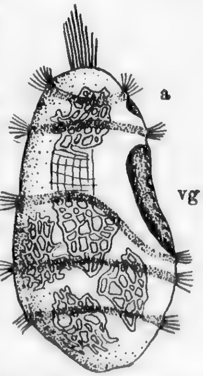


FIG. 253.—LARVA OF *Antedon* (combination of figures by THOMPSON AND GOETHE after KORSCHELT AND HEIDER).

II. Class **Asteroidea.**

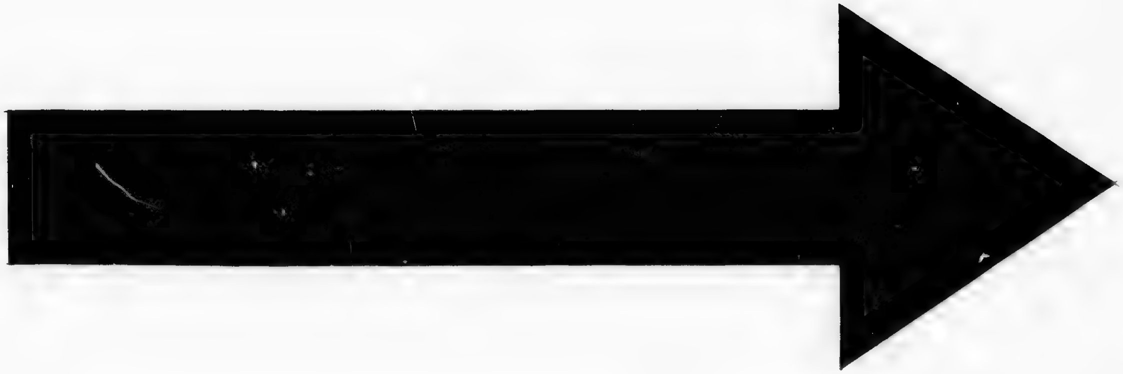
The Asteroidea, or Starfishes, are all flattened forms, at no period of their lives attached by a stalk, but creeping about freely upon the oral surface. In some forms the body is a flattened disk pentagonal in outline (*Asterina*), but more usually (Fig. 246) the five radii are prolonged out into five stout unbranched arms, and in some forms, such as *Brisinga*, the arms may be long and slender and more than five in number. The mouth is situated in the centre of the oral surface, and the anus slightly excentrically upon the aboral surface, while the hydrocœl system of tubes is confined, as in the Crinoids, to the oral surface of the body, except that the madreporiform tubercle by which the system communicates with the exterior is upon the aboral surface in the interradius *CD*.

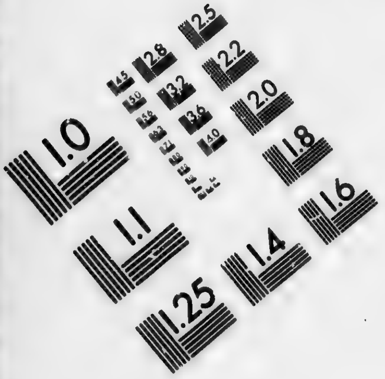
The ectoderm is throughout ciliated, and contains usually numerous mucous glands, while in its lower layers ganglion-cells and nerve-fibrils form a plexus extending over the entire surface of the body.

Calcareous matter is deposited in the connective tissue, but in the majority of forms the primitive apical plates are not recognizable in the adult; more usually the aboral surface is covered by a large number of small plates arranged without any regularity, or else the calcareous matter forms a reticulum composed of numerous fused bars, short spines rising frequently from the points of union. In embryos, however, and in some adult forms, such as *Zoroaster* (Fig. 247), the apical system can readily be made out, and consists of a centrodorsal plate (Fig. 247, *CD*), sometimes grooved upon the edge for the anus (*an*), surrounded by five under-basals (2) usually small, alternating with which are five basals (3). At the base of each arm is a radial (4), and in embryos beyond this there is in each radius another plate, which as growth takes place is carried further and further from the radial and finally forms the *terminal plate* (*T*) of the arm, by which name it is known.

Of the oral system the orals are possibly represented by the so-called odontophore plates, which are generally small and in many cases covered over by other plates of the oral surface, and lie in the immediate neighborhood of the mouth. At the junction of the oral and aboral surfaces of the disk and arms two series of plates are frequently to be found which from their position are termed the *supra* and *infra-marginals*, and, in addition to these, series of plates with definite arrangement are developed in connection with the water vascular system. Thus along each side of the middle line of each arm is a series of plates, which, sloping aborally and towards the axis of the arm, meet to form the floor of an ambulacral groove which extends outwards from the mouth to the extremity of the arm. These are the *ambulacral plates* (Fig. 254, *A*), and each series of them is flanked upon the outer side by a row of *adambulacrals* (Fig. 254, *B*) whose number may or may not correspond with that of the ambulacrals. Between the adambulacral series of adjacent arms a series of plates may be interposed upon the oral surface of the disk, and to these the name of *interambulacrals* may be applied.

Spines are very frequently borne by the plates or reticulum of the aboral surface, but are usually low and immovable, though upon the marginal and adambulacral plates they are very frequently longer, united to the plates by a rudimentary articular surface and supplied with muscle-fibres by which they can be moved. In addition to these appendages of the dermal skeleton, others are to be found in the Starfishes, such, for example, as the ciliated spines found in a few forms, such as *Luidia*, upon the marginal plates. These spines are small and delicate, and grouped together, their principal peculiarity being that they are covered by an epithelium of high columnar cells which bear strong cilia. In most Starfish also peculiar structures termed *pedicellariæ* are developed in connection with the skeleton, but their description may be deferred until the Echinoids are under discussion, in which group they reach a high grade of development. Peculiar to certain genera of Starfishes, e.g. *Luidia*, are the *paxillæ*, found principally upon the aboral surface of the body. They consist of small columns of carbonate of





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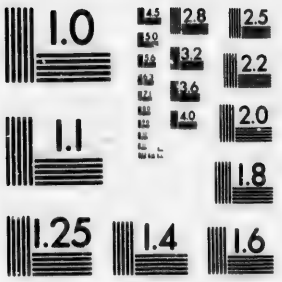
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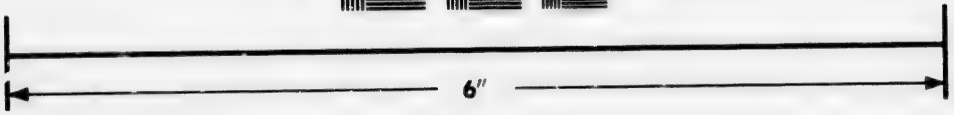

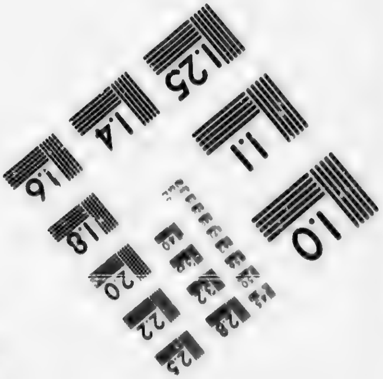

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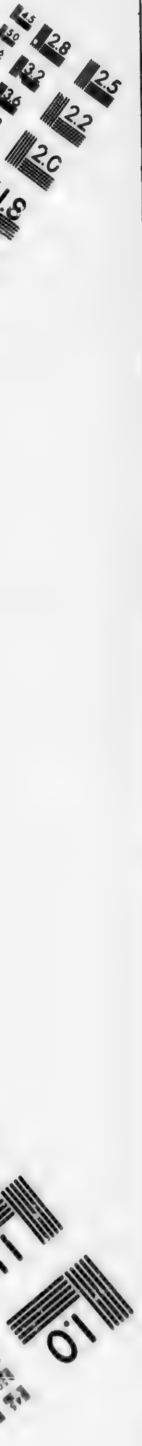
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lime imbedded in the connective tissue, and bear upon their free extremity a number of radiating spines, which vary in the amount of movement of which they are capable in different species. The paxillæ are frequently found in groups around the dermal branchiæ, over which the spines may be bent so as to serve for protection.

These dermal branchiæ (Fig. 254, *b*) are pouchlike evaginations of the cœlomic cavity with thin walls composed of ectoderm and a layer of ciliated cells continuous with the peritoneal lining of the cœlom, between these two layers there being but a slight development of connective tissue and circular and longitudinal muscle-fibres. These pouches are scattered plentifully over the aboral surface, and in some forms occur upon the oral surface also. Their thin walls and the extent of surface they collectively represent leave little room for doubt but that they possess respiratory functions, though they may also serve indirectly in excretion, since it has been asserted that the amœboid cells of the cœlomic hæmo-

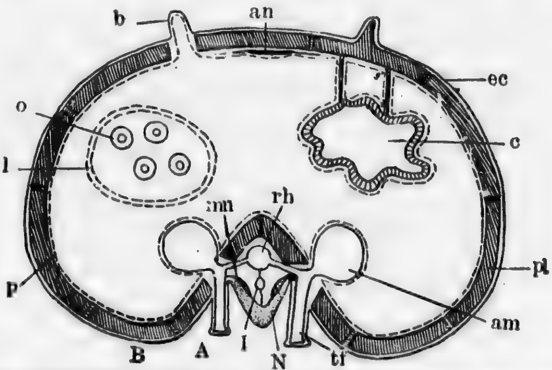

FIG. 254.—TRANSVERSE SECTION OF ARM OF A STARFISH (modified from LUDWIG).

A = ambulacral plate.
am = ampulla.
an = aboral nerve.
B = adambulacral plate.
b = branchia.
c = digestive cæcum.
ec = ectoderm.
l = schizocœlic sinus.
mn = muscular nervous system.
N = epithelial nervous system.
o = ovum.
p = peritoneal epithelium.
pl = calcareous plate.
rh = radial hydrocœl-vessel.
tf = tube-foot.

lymph, laden with excretory particles, migrate to the exterior through the walls of the branchiæ.

The calcareous plates are imbedded in a connective tissue usually of considerable thickness and sometimes of a high degree of consistency. Upon its inner side are to be found circular and longitudinal bands of muscles, especially developed in the arms, which are capable of considerable movement.

The general cœlom is traversed by mesenteries extending from the body-wall to the digestive tract, which do not require, however, a detailed description. Suffice it to say that each radial cæcum of the digestive tract which extends out into the arm is suspended by two longitudinal mesenteries (Fig. 254) which, with the body-wall and cæcum, enclose a canal opening proximally into the general cœlom. Extending vertically through the cœlom in the interradius *CD* is a cavity with strong walls which is in communication with the exterior by the madreporiform tubercle and is the axial sinus. This is a portion of the cœlom which is early separated from the rest, and in the embryo opens to the exterior by the water-pore, the stone-canal opening into it. In the adult the cavity of the sinus is fairly spacious and contains the ovoid gland suspended to its walls by a mesentery. Prolongations of the sinus accompany the genital rachis and, enclosing the reproductive organs, form the genital sinuses.

The schizocœlic system consists of an oral ring lying between the nervous and water vascular rings, and of five radial vessels which pass out from this along the axes of the arms. The oral ring is divided by an oblique septum into two portions, one of which lies upon the aboral surface of the other, and enters into connection with the axial sinus, the ovoid gland abutting upon the septum in one of the interradii. The oral sinus also communicates with the cœlom by five interradial orifices. The radial sinuses are divided into two cavities by a median longitudinal septum, and, like the oral sinus, communicate with the cœlom. A lacunar system, such as occurs in the Crinoids, is not developed in the Asteroidea, though certain spaces in the wall of the ovoid gland and its prolongations are perhaps representatives of it. The ovoid gland is formed of loose connective-tissue trabeculæ, which are covered by cells frequently found in active division, and are supposed to become the amœboid corpuscles of the cœlom and blood system.

The hydrocœl consists as usual of an oral ring and five radial canals, the latter lying at the bottom of the ambulacral grooves and therefore external to the ambulacral plates (Fig. 254, *rh*). Between each pair of plates a branch passes upwards (i.e., aborally), and dilates into a globular sac, the ampulla (Figs. 254 and 255, *am*), which is occasionally double, and from this a cylindrical tentaclelike process passes outwards again between two plates forming extensible processes (Fig. 254, *tb*) equivalent to the tentacles of the Crinoids. These processes in some of the more primitive forms, such as *Luidia* and *Astropecten*, and the terminal ones at the extremity of the arms of all forms, are conical in shape, but more usually the great majority of them are provided at their extremities with sucking disks, whereby they can adhere to foreign bodies and serve thus as locomotor organs. Hence they are known as the tube-feet or ambulacra. In some forms they are arranged in two rows, one on each side of the axis of the arm, but in others, as for example the common Starfish *Asterias*, the successive feet of each row alternate with each other, so that they have the appearance of being arranged in four rows. By means of the muscles of the wall of the ampullæ water can be forced into the tube-feet, which may be thus extended, a circular valve occurring in the branch which passes from the radial canal to the ampulla preventing the water from passing back into the canal. Contrary to what occurs in the Crinoids, there are several appendages to the oral ring, in addition to the stone-canal. This leaves the ring in the interradius (*D* and, passing aborally, communicates with the axial sinus which, as already stated, opens to the exterior by the madreporite. This is a complicated calcareous sieve-plate of some thickness, and the union of the canal and the sinus takes place within its substance, so that in reality the canal seems to open to the exterior. The embryonic history, and the fact that injections forced through the tubercle pass into both the sinus and the canal, show that what has been described is the true relationship. In the walls of the stone-canal calcareous matter is deposited, whence the name applied to it, and its walls form projections extending into the lumen of the canal, the surface for the ciliated epithelium being thus increased.

The appendages of the oral ring are of two kinds, both being situated in the interradii, that containing the stone-canal, however, usually lacking any other appendage. In some forms hollow saclike structures open into the ring by a narrow neck, and are termed the Polian vesicles; their walls consist of connective tissue in which are situated muscle-fibres, and their interior is lined by an epithelium which appears to separate and give rise to the amœboid cells of the hydrocœl fluid. The other kind of appendages occur generally throughout the group and are known as Tiedeman's vesicles, consisting of masses of hollow tubes arranged in pairs in one or more of the interradii. The epithelium lining the walls of these structures also seems to give rise to the amœboid cells, both kinds of organs being therefore comparable to lymphatic glands, though the Polian vesicles have also been regarded as reservoirs for the hydrocœl fluid.

The mouth is situated at the centre of the oral surface of the disk, and opens into a short œsophagus which, in some forms, has connected with it ten glandular pouches. The œsophagus opens into a usually capacious cardiac stomach which is frequently lobed (Fig. 255, *c*), is eversible and provided with special muscles for its retraction. Above this comes the pyloric stomach which gives rise to five radial pouches, which soon branch into a pair of sacculated pouches extending out into the arms, and being termed the radial cæca (*l*). From the pyloric stomach a short rectum passes aborally, interradial cæca being sometimes found close to its origin from the pyloric stomach, and opens upon the dorsal surface. In a few forms, such as *Luidia*, *Astropecten*, and their allies, the anus is wanting, but more usually it is present in the region indicated.

The epithelial nervous system consists of a plexus of ganglion-cells and fibres imbedded in the ectoderm and covering the surface of the body, and of an oral ring and five radial nerves (Fig. 254, *N*) which, as in the Crinoids, are situated in the lower layers of the ectoderm. Upon the aboral surface of the oral ring and the radial nerves sections show distinct bands of fibres separated from the ring and nerves by a delicate layer of connective tissue; these constitute the muscular system of nerves (Fig. 254, *mn*), and their branches appear to be supplied to the muscles of the body-wall and of the ampullæ and tube-feet. The aboral system is but feebly developed when compared with that of the Crinoids. A transverse section of an arm shows lying between the muscles of the aboral surface and the peritoneal mesoderm a cord of nerve-fibres (Fig. 254, *an*), the five cords converging towards the centre of the aboral surface of the body, the entire system forming thus a five-rayed star. In position and general relations this system of nerve-cords is directly comparable to the aboral system of the Crinoids, and may be regarded as homologous with it.

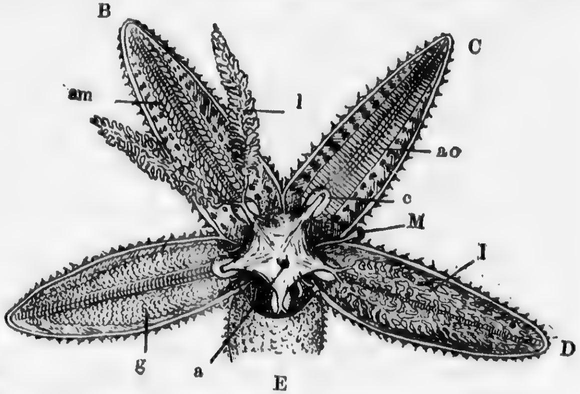

FIG. 255.—A STARFISH, *Asteracanthion*, WITH THE INTEGUMENT OF THE DISK AND RAYS REMOVED TO SHOW THE INTERNAL STRUCTURE.

a = anus.
am = ampullæ of tube-feet.
ao = ambulacral ossicles.
c = cardiac pouch of stomach.
g = reproductive organ.
l = liver cæca.
M = madreporite.
A–E = the five radii.

Special sense-organs are represented by the terminal tentacles of the radial hydrocœl canals, which, as already stated, retain a tentacle-like form and do not develop suckers at the extremity. Their walls are richly supplied with nerves, and they are surrounded and may be covered in by the movable spines of the adambulacral and marginal plates. That they have a sensory function seems clear, but what the exact nature of the function may be is as yet uncertain. At the base of the terminal tentacle of each arm is situated an eye, consisting of a large number of conical depressions, lined by an epithelium containing a red pigment, covered on the outside by a cuticle and richly supplied with nerve-fibrils. There do not seem to be present any refractive structures other than the cuticle, and these eyes can only convey to the animal impressions of changes in the intensity of the light falling upon them; they cannot form images of external objects.

The reproductive organs are ten in number, two being situated in each arm (Fig. 255, *g*). Each consists of a mass of reproductive cells, and is enclosed in a genital sinus (Fig. 254, *l*), which, as already stated, communicates with the axial sinus. The proximal end of each gland is connected with a cordlike structure, the genital cord or rachis, the ten cords uniting in a ring situated beneath the aboral surface of the body, a cord passing orally from this ring to unite with the tissue of the ovoid gland. The genital sinuses accompany the cords, enclose the ring, and pass to the axial sinus along with the descending cord. A connection therefore exists between the reproductive organs and the ovoid gland, just as in the Crinoids, and indeed the reproductive organs arise in the embryo from an outgrowth of the ovoid gland. In reality the genital cords are tubes containing in their interior immature reproductive cells which seem to migrate from the ovoid gland to the reproductive organs where they become mature. The reproductive openings are usually placed upon the aboral surface (*Asterina* forming an exception) of the arms or disk in the interradii; a single pore usually exists for each gland, and occasionally there may be several.

Development of the Asteroidea.—The larval forms of the Starfishes are known as the *Bipinnaria* and *Brachiolaria*. The former has a somewhat triangular shape, the apex of the triangle being the anterior extremity, and in the middle of the ventral surface is a deep concavity in which the mouth opens. The posterior border of the concavity is formed by a band of cilia which is continued around the lobed sides of the body to the anterior extremity, forming a postoral ciliated band, the anus lying without the area enclosed by it. In front of the mouth is a trilobed region also surrounded by a band of cilia, the adoral band. In young embryos the adoral and postoral bands are united at the apex, separation only supervening later. In later stages two additional arms are developed at the sides of the apical lobe, which becomes like the new arms destitute of cilia, and tipped with a group of wartlike elevations. This form of the larva is known as the *Brachiolaria.*

A peculiar process, amounting almost to a metamorphosis, occurs during the transformation of the larva into the Starfish. Calcareous plates of the aboral system make their appearance on the dorsal surface of the stomach near the posterior end of the body, and oral plates on the ventral surface of the same organ. These two systems, at first rather widely separated, gradually approach each other, and at the same time the internal organs assume the adult form. Finally the two series of plates unite, enclosing between them the hydrocœl, a portion of the digestive tract and of the cœlom. The original mouth and anus are obliterated, and indeed the anterior half of the larva takes no part in the formation of the adult animal, but is gradually absorbed.

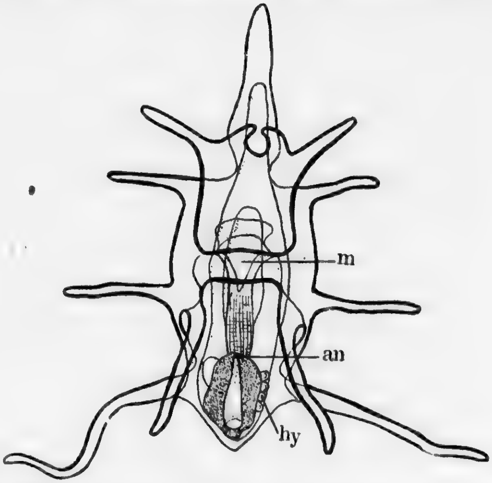

Fig. 256.—Bipinnaria of *Asteracanthion* (after Agassiz).
an = anus. *hy* = hydrocœl. *m* = mouth.

A highly-developed faculty for regeneration occurs in the Asteroidea, the disk being able to regenerate lost arms; and indeed an arm, with which a small fragment of the disk is in connection, has the power of regenerating all the missing parts. Specimens of the common Starfish *Asterias* are in consequence frequently found with one or more of the arms bifid at the tip, or even with an abnormal number of arms.

III. CLASS **OPHIUROIDEA.**

The Ophiuroidea, or Brittle-stars, resemble the starfishes closely in their general form, consisting of a central disk from which five arms radiate (Fig. 257). The arms, however, are in all cases slender and distinctly marked off from the disk, and in *Astrophyton* branch dichotomously. Closer examination reveals, however, considerable differences from the Starfishes; there is no anus, the madreporite is on the oral surface, there are no visible ambulacral grooves on the arms, which are more or less circular in section and do not contain cæcal processes of the digestive tract. Furthermore, on each side of each of the five radii there is upon the edge of the oral surface of the disk a slitlike opening, divided into two parts in *Ophioderma*, and leading into a thin-walled ciliated sac, which is to be regarded as an invagination of the wall of the body. There are thus ten of these *genital bursæ* as they are termed, two being situated in each interradius. They seem to have a respiratory function, and serve also for the exit of the reproductive elements, in some forms, e.g. *Am-*

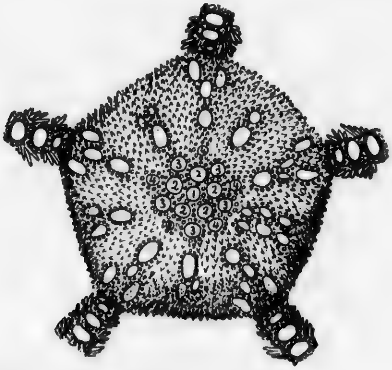

FIG. 257.—*Ophioglypha aculeata* FROM THE ABORAL SURFACE TO SHOW THE PERSISTENT APICAL SYSTEM OF PLATES.
(The arms are cut off close to the disk).

1 = centrodorsal plate.
2 = under basals.
3 = basals.
4 = radials.

phiura squamata, even serving as brood-pouches in which the young develop.

The ectoderm is indistinguishable over the greater portion of the body in the adults, becoming, as in the Crinoids, confounded with the mesoderm. Calcareous plates are largely developed in this tissue (except in *Ophiomyxa* and its allies), giving to the disk and arms a brittleness which has suggested the popular name for the group. The extent to which the apical system of plates is distinguishable in the adults varies considerably even in members of the same group, and while in some forms (Fig. 257) all the plates represented in the Starfish *Zoroaster* can be distinguished, in others only the radials or the basals or both are visible. At the tip of each arm is a plate comparable to the terminal of the Asteroidea, and in addition there are frequently present series of interradials or interbrachials, the most aboral plates of which separate the radials from each other and extend round to the oral surface, abutting on five large plates known as the *buccal shields* and corresponding to the orals of other forms. On the aboral surface of the disk above the origin of each arm there is a pair of plates termed the radial shields, which must not, however, be confused with the radial plates extending along the aboral surfaces of the arms.

These latter form a complete series extending from the disk to the terminal plates, and form the aboral wall of the arms, their lateral walls being formed by another series of plates, the *adambulacrals* (Fig. 258, *Ad*), while still another series, the *superambulacrals*, form their oral walls. Between each adambulacral plate and its successor is a pore (usually bounded by a number of small plates) through which the tube-feet are protruded, the radial water-vascular canals being situated in the interior of the arm. The cavity of the arms is occupied almost entirely by a linear series of calcareous masses termed the *vertebral* or *ambulacral ossicles* (Figs. 258 and 260, *A*), each of which consists of two halves, usually firmly united by suture. The ossicles are united by well-developed articular surfaces, and have attached to them muscles, whereby a considerable amount of motion is possible for the arms as a whole, the motion being almost entirely in a horizontal plane, except in *Astrophyton* and its allies, in which the arms may be coiled up over the oral surface, in a manner similar to what is found in the Crinoids. These ambulacral ossicles seem to correspond with the similarly-named plates of the Asteroidea.

In the neighborhood of the mouth certain modifications in the arrangement of some of these plates occur. The two halves of each first ambulacral ossicle (Fig. 258, A_1) are widely separated, and come into close relation with the similarly-separated ossicles of adjacent radii, forming a buccal shield. The plate so formed rests upon the aboral surface of the first adambulacrals (Ad_1), which unite in pairs in a similar manner, forming a triangular plate, termed an *oral angle-piece*, lying in an interradius, and partly covered on its oral surface by a buccal shield. At the sides of the buccal shield are the so-called *lateral buccal shields* (Ad_2), which are in reality the second adambulacrals of adjacent arms, and cover in the second ambulacrals (A_2), which serve as supports for the oral angle-piece. Along the margins of the oral surface of this are a series of spines, the *buccal papillæ*, while, at the apex of the triangle, are the *dental papillæ*. The vertical edge of the piece is furnished with a number of stout projections, the

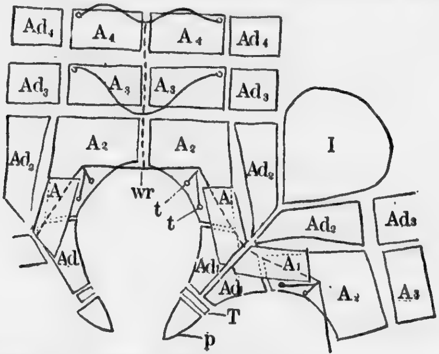

FIG. 258.—DIAGRAM TO SHOW THE ARRANGEMENT OF THE CIRCUMORAL PLATES OF AN OPHIURAN (after LUDWIG).

A = ambulacral plates.
Ad = adambulacrals.
I = interradial.
p = pala angularis.
T = torus.
t = oral tentacles.
wr = radial hydrocœl-vessel.

palæ angulares (Fig. 260, *p*), whose bases generally fuse to form a supporting plate, the *torus angularis* (*T*).

Spines developed in connection with the dermal skeleton, leaving out of consideration the oral angle-pieces, may be entirely wanting, but in many forms they are borne in vertical rows upon the adambulacrals, and are usually movable. In a few forms, especially those inhabiting rocky bottoms, peculiar hooked spines are situated on the oral surface of the arms towards their extremities, and seem to serve an adhesive function. Pedicellariæ are absent, except in *Astrophyton* and allied genera.

The cœlom (Fig. 260, *c*) is of comparatively slight extent, the cavity of the disk being largely occupied by the digestive tract, and that of the arms by the ambulacral ossicles. In the disk the cavity is traversed by numerous bands which extend from the body-wall to the wall of the digestive sac, and from the wall of the œsophagus a membrane extends outwards and orally to be attached to the peribuccal plates, forming a septum (Fig. 260, *s*), enclosing a cavity surrounding the œsophagus, the peripharyngeal space (*ps*), which is completely separated from the rest of the cœlom. In *Ophiothrix* and some other forms a second septum occurs parallel to the one just mentioned, so that the peripharyngeal space is double. The cœlom of the arms consists of two portions, one lying on the aboral and the other on the oral side of the series of ambulacral ossicles. The aboral cavity is expanded laterally so as to partially surround the ossicles, but this lateral portion is traversed opposite each ossicle by a calcareous lamella, and is thus separated into a series of chambers which open into the undivided aboral portion, termed the aboral or dorsal canal. An axial sinus, standing in close relationship to the ovoid gland, exists, but presents some features not found in the Asteroidea. It consists in *Amphiura squamata* (Fig. 259) of three distinct portions completely separated from one another; one of these is the so-called ampulla (*am*) of the stone-canal; the second (*s*) lies in close relation to the ovoid gland, which is developed on its axial wall; while the third is comparatively small, and is associated with the genital cords (*gr*), and the mass of cells in the ovoid gland from which these arise. These two last cavities are said to be portions of the general cœlom which become separated off during development, and are not simple extensions of that portion of the cœlom into which the stone-canal opens in the embryo, and which persists as the ampulla.

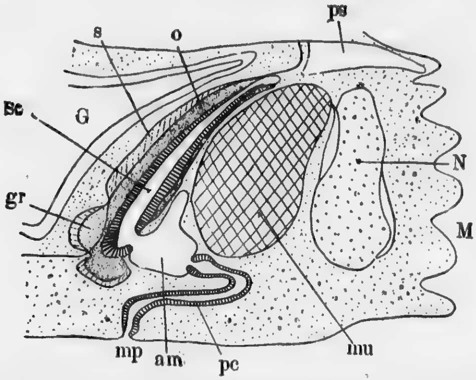

FIG. 259.—DIAGRAM SHOWING THE RELATIONSHIPS OF THE STONE-CANAL, AXIAL SINUS, ETC., IN *Amphiura squamata* (after MACBRIDE).

am = ampulla of stone-canal.
G = genital bursa.
gr = origin of genital rachis.
M = mouth.
mp = madreporite.
mu = muscle.
N = ring-nerve.
o = ovoid gland.
pc = pore-canal.
ps = peripharyngeal space.
s = sinus.
sc = stone-canal.

These differences from what occurs in the Asteroidea do not imply, however, a want of homology between the axial sinuses of the two groups. The entire sinus is after all a separated portion of the cœlom, and it makes little difference whether it be all separated off at an early stage in the development, as in the Asteroidea, or only a part of it, the rest developing later from the general cœlom as in the Ophiuroidea and Crinoidea, the dorsal organ of the latter being homologous with the axial sinus *minus* the ampulla of the stone-canal of the Ophiuroidea and Asteroidea.

Lying on the aboral surface of each radial nerve-cord is a radial schizocœlic sinus (Fig. 260, *br*), which communicates with an oral sinus surrounding the mouth. The relations of this system are similar to those of the schizocœlic system of the Asteroidea, and numerous communications between it and the cœlomic cavities occur. It contains, however, a system of canals, which correspond to the lacunæ occurring in the walls of the œsophagus in the Crinoids. They have been termed blood-vessels in the Ophiuroidea, the sinuses which surround them being termed the perihæmal canals; they follow the course of these latter, a process of the ovoid gland coming into connection with the oral lacunar ring. This gland (Fig. 259, *o*) is, as in other groups, partly associated with the lacunar system and partly with the genital apparatus. It lies in the wall of the axial sinus and projects into it so as almost to fill it. At one extremity, as stated, it comes into connection with the oral lacunar ring, and at one point in its wall it contains a mass of cells from which the genital cords pass out to the reproductive organs, accompanied by strands of the lacunar tissue.

The hydrocœl has the usual arrangement, and is confined to the oral surface of the disk and arms. The radial canals (Fig. 260, *wr*) lie on the oral surface of the ambulacral ossicles, extending to the terminal plate, and ending, at least in those forms which have simple arms, in a terminal tentacle. At regular intervals, corresponding in number to the ambulacral ossicles, the radial canals give off transverse branches, which pass outwards in the substance of the ossicles (Fig. 258), and make their exit through the ambulacral pores between successive adambulacral plates to terminate as tube-feet. No ampullæ occur on these transverse branches, though a circular valve occurs just where each branch becomes continuous with the tube-foot. The feet are simple conical structures destitute of a terminal sucker, and do not therefore serve for locomotion. Their walls are richly supplied with nerves, and in some forms are provided with numerous papillæ apparently sensory in function. Surrounding the mouth are ten buccal tentacles (Fig. 260, *bt*), which correspond to the first two pairs of tube-feet of each radius of the Asteroids, but arise by fine branches, which later divide, and are directly connected with the oral ring-canal (Fig. 258, *t*). These seem to be undoubtedly sensory and perhaps olfactory in function. The oral ring-canal usually has attached to it in each interradius, except that in which the stone-canal lies, a single Polian vesicle (Fig. 260, *PV*), though in *Ophiactis* two, three, or even four vesicles may occur in each interradius. The stone-canal, as has been noted, opens into a special portion of the cœlom, the ampulla of the stone-canal, and this again communicates with the exterior by a tube opening by a pore placed in the adults on the oral surface of the body in one of the buccal shields; primitively the opening is situated on the aboral surface, only later migrating to its final position. In *Astrophyton*, in which the buccal shields are wanting, the madreporiform tubercle occurs on the oral surface of the disk in one of the interradii, and in some species there may be five tubercles, one in each interradius, a multiplication of the pores and stone-canals occurring also in other genera, such as *Amphiura* and *Ophiolepis*.

In consequence of the position of the pore or tubercle the position of the stone-canal in the Ophiuroidea is very different from that which it possesses in other groups. Whereas in these it passes aborally from the water vascular ring, in the Brittle-stars it hangs down from the ring towards the oral surface of the body. All those structures too, such as the axial sinus and the ovoid gland, which are usually associated with the canal, undergo a similar transformation of position, which is possible on account of the distance from the oral surface at which the water vascular ring is situated (see Fig. 259).

The digestive tract is very simple. The mouth guarded by the oral angle-pieces opens into a short œsophagus (Fig. 260, *O*), which communicates with a capacious saclike stomach, slightly pouched out in each radius, but not extending into the cavities of the arms. There is no anus in any member of the group.

The epithelial nervous system of the Ophiuroidea is associated with the general ectoderm in very young specimens, but later sinks into the cavity of the body by a process which may be compared to an invagination. Consequently a tube is formed lying within the body-wall on the oral surface of the body, the radial nerves (Fig. 260, *nr*) being situated in its aboral wall. This tube forms the *epineural sinus*, and the cavity it encloses seems to be in reality a portion of the exterior, though it may be schizocœlic. The oral ring of the nervous system is not enclosed in an epineural canal, but remains in connection with the ectoderm at the lower extremity of the œsophagus, being pushed thus aborally by the development of the oral angle-pieces. The radial nerves are, however, contained in the wall of the sinus, coming to the surface of the body at the tips of the arms, where they terminate by fusing with the general ectoderm. The muscular nervous system is, as in the Asteroidea, closely associated with the oral ring and radial nerves, lying on their aboral surface and separated from them only by a thin layer of connective tissue. The aboral system consists of a ring situated beneath the aboral surface of the body, from which branches pass off towards the reproductive organs. Indeed the entire system is intimately associated with the genital cords, and its course can be understood from a description of these structures. No special sense-organs other than the terminal and buccal tentacles and the tube-feet, already described, occur in the Ophiuroidea.

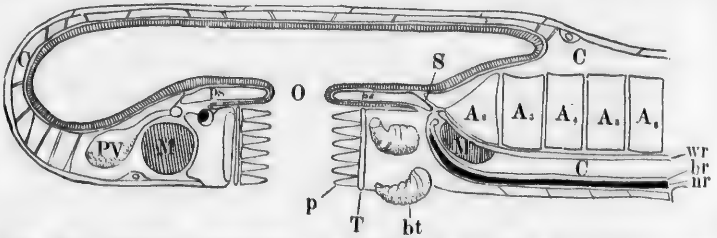

FIG. 260.—SECTION THROUGH AN OPHIURAN SHOWING STRUCTURE (after LUDWIG).

A = ambulacral ossicles.
br = schizocœlic sinus.
bt = buccal tentacles.
C = cœlom.
M = muscle.
nr = radial nerve.

O = mouth.
p = pala angularis.
ps = peripharyngeal space.
PV = Polian vesicle.
S = peripharyngeal septum
T = torus angularis.

wr = hydrocœl-vessel.

As already stated, the genital cord arises from a group of cells in the wall of the ovoid gland (Fig. 259, *gr*) and passes in an interradius towards the aboral surface of the body, carrying with it a portion of the axial sinus. Arrived at this point the sinus and cord form rings, the aboral nerve-ring lying in the wall of the sinus, while the genital cord lies in its interior, attached to its wall by a lamella of connective tissue. From the genital-cord ring ten short branches are given off which enlarge into ten saclike reproductive organs, lying in close contact with the walls of the genital bursæ. The ova and spermatozoa migrate from their point of origin in the ovoid gland along the genital cords, which also contain prolongations of the lacunar tissue of the gland, and mature in the reproductive pouches. During the spawning-time the lobes of the reproductive organs protrude into the bursæ, pushing before them the thin walls of these pouches, and the reproductive elements when mature burst through into the cavities of the bursæ, whence they make their way to the exterior, or else, as in *Amphiura squamata*, undergo their development in the pouches.

From what has been said it may be seen that the genus *Astrophyton* and its allies differ in many respects from the other Ophiuroids, having arms sometimes branched and capable of being curled in over the oral surface, possessing pedicellariæ and lacking buccal shields, not to mention other peculiarities. Consequently the class Ophiuroidea may be regarded as consisting of two orders, the **EURYALIDA**, including *Astrophyton*, commonly known as the Basket-star, *Trichaster*, in which the arms do not branch, and other similar forms, and the **OPHIURIDA**, which includes the other genera, such as *Ophiothrix*, *Ophioderma*, *Ophiolepis*, *Amphiura*, etc.

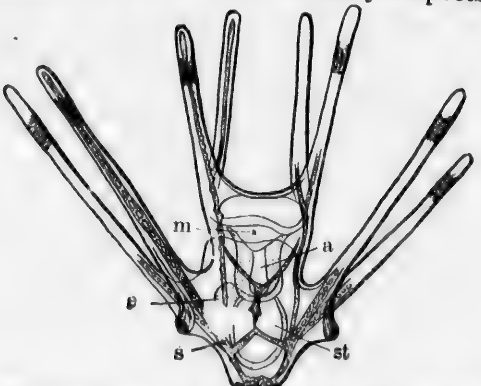

FIG. 261.—PLUTEUS LARVA OF *Echinarachnius parma* (after FEWKES).

a = œsophagus.
e = rudiment of adult.
m = mouth.
s = calcareous skeleton.
st = stomach.

Development of the Ophiuroidea.—Except in a few cases, such as *Amphiura squamata*, whose habits have already been referred to, the development of the young Ophiuran takes place outside the body of the parent in the surrounding water and a typical larval form occurs. This is known as the *Pluteus* (Fig. 261) and in its general form resembles the Bipinnaria of the Starfish. The ciliated band, however, does not divide into an adoral and a postoral portion, but remains continuous, and the lateral lobes become long armlike processes supported by a special skeleton, formed of calcareous rods developed in their interior. The mode of development of the young Ophiuran from this larva resembles closely that described for the Asteroidea.

CLASS IV. **ECHINOIDEA.**

The Echinoidea present greater differences in shape than are found in any of the other groups of Echinoderms, being more or less spherical, oval, discoid, pentagonal, or heart-shaped, but they are all characterized by the absence of arms, by the calcareous plates being immovably united (except in a few forms, such as *Asthenosoma*, where their edges overlap and they are consequently movable) to form a firm test, and by a great development of movable spines upon the plates, whence the popular name of Sea-urchins usually applied to members of the group. The test is covered by ciliated ectoderm, below which is a plexus of nerve-fibres and ganglion-cells which coördinate the movements of the spines, to whose bases muscle-fibres are attached.

The test presents certain variations in the different forms, but there are also certain features which are to be considered typical for the group. The apical system of plates is usually well developed. A centrodorsal is present in the genus *Salenia*, but in all other recent forms it is replaced by a series of small plates which constitute the *periproct* in the simpler forms, since in these they surround the anus. These plates are surrounded by a circle of five basals (Fig. 262, *g*), usually termed genitals on account of the reproductive ducts opening by a pore upon them. The five radials (*o*) are also represented, alternating with the basals; and since the terminal tentacle of the radial hydrocœl-canals protrudes through a pore situated upon them, and more especially since a pigment-spot, supposed to be an eye, lies frequently at the base of this tentacle, these plates are usually known in this group as the oculars. Starting from each ocular and each genital, rows of plates pass outwards and downwards towards the mouth, the test being formed of twenty such rows extending in meridional lines from the aboral to the vicinity of the oral pole. The rows are grouped together in pairs, five of the pairs starting from the genital plates and the other five from the oculars; and since a number of the plates in these latter rows are perforated for the emission of tube-feet, they are generally known as the ambulacral plates (Fig. 262, *A*), while those of the intervening pairs are termed the interambulacrals (*I*). The pores for the tube-feet are almost always double, and are situated usually near that side of a plate which abuts upon the adjacent interambulacral; in some forms but a single pair of pores occurs on each plate, but more usually two or more pairs are found (Fig. 262)—an arrangement which indicates that such plates are formed by a fusion of several smaller ones, each of which is represented by one of the pairs of pores.

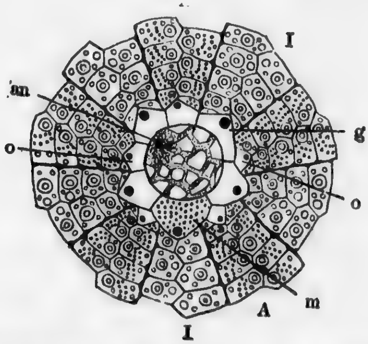

FIG. 262.—FIGURE SHOWING THE ARRANGEMENT OF THE APICAL SYSTEM OF PLATES OF *Strongylocentrotus*.

A = ambulacral areas.
an = anus.
g = genital plates.
I = interambulacral areas.
m = madreporite.
o = ocular plates.

In the more primitive forms one of the genital plates is transformed into the madreporiform tubercle (Fig. 262, *m*), but in others the limits of the tubercle may extend so as to include all the plates of the apical system, and at the same time the anal opening may leave its position near the centre of the apical system and become situated in the interradius AB, either at the margin of the flattened disklike test, or even on its oral surface. A marked bilaterality of form is thus developed, which may become still more pronounced by a migration of the mouth away from the centre of the oral surface along the line of the radius D, which at the same time becomes more or less altered in size and form, and consequently dissimilar to the other radii (Fig. 263). In these cases it is possible to recognize in addition to oral and aboral surfaces anterior and posterior poles and a right and left side, the median line of the body passing in front through the radius D and posteriorly through the interradius AB. Three of the radii, C, D, and E, thus lie in the anterior half of the body, and for descriptive purposes these have been termed the *trivium*, while the two posterior ones, A and B, constitute the *bivium*.

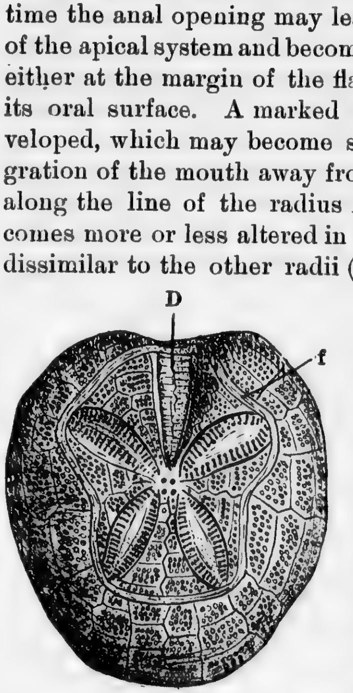

FIG. 263.—A PETALOSTICHOUS ECHINOID, *Brissopsis lyrifera*, FROM THE ABORAL SURFACE WITH THE SPINES REMOVED (after A. AGASSIZ).
D = modified ambulacrum.
f = fasciole.

The mouth, which is usually situated in the centre of the aboral surface, is surrounded by an area, the peristome, which has imbedded in it only a few scattered calcareous plates and consequently possesses a somewhat leathery consistency. An oral system of plates cannot be distinguished in adult Echinoids.

The marked bilateral symmetry referred to above as occurring in certain Echinoids is undoubtedly a secondary condition, those forms in which the mouth is central and the anus approximately so, and whose bilaterality is indicated only by the madreporiform tubercle, being, there is every reason to believe, the most primitive. The bilaterality cannot be regarded as a reversion to the more primitive symmetry of the larva, since in the latter the hydrocœl-pore lies to the left of the median line, while in the bilateral Echinoids it is situated in the right anterior interradius. Nor can it be regarded as indicating a primitive adult symmetry, which, though usually disguised, exists in all the Echinoderms, since, as stated, the forms in which it is most pronounced are the most highly differentiated members of their group. It should be mentioned that in the less differentiated forms the radiality is disturbed by the arrangement of the plates bordering upon the peristome, as well as by the unpaired madreporiform tubercle. For if the rows of plates of each ambulacral region be indicated alternately *a* and *b*, proceeding contrary to the direction of the hands of a watch, so that the posterior interambulacral region is bordered by the plates *Ba* and *Ab*, then it will be found that the plates bordering the peristome in the rows *Ab*, *Ba*, *Ca*, *Db*, and *Ea* are large and usually pierced by a double pore, while those of the rows *Aa*, *Bb*, *Cb*, *Da*, and *Eb* are smaller and pierced usually by only one pore. This arrangement does not, however, necessarily point to any special plane of bilaterality, but is interesting on account of its constant occurrence in both the bilateral and the more radial forms, whence it furnishes a means of identifying the plane of bilaterality in the latter.

Projecting inwards from the inner surface of the test in the neighborhood of the peristome are frequently to be found calcareous plate- or pillar-like processes termed *auriculæ* (Fig. 265, *au*), which may either be confined to the interambulacral plates or occur also on the ambulacrals, uniting in some forms, such as *Strongylocentrotus*, in pairs, so as to form arches through which the radial hydrocœl-canals and nerve-cords pass. In the flattened disklike forms, such as *Echinarachnius*, these pillars are much more numerous, extending from the oral to the aboral surfaces of the test. Attached to the outer surface of the test are numerous spines, each of which is hollowed out at its base, the hollow fitting over the convexity of a tubercle upon the test. This ball-and-socket articulation allows of a free movement of the spines in any direction, a movement which is effected by muscles extending from the test to the base of each spine, and forming a sheath around its base. The spines thus serve as efficient organs of locomotion, usurping this function entirely in some forms, while in others they are aided by the tube-feet. They also in some forms serve as defensive structures, as in *Diadema*, where they are long and slender and readily penetrate the skin of less-protected animals, or in *Asthenosoma*, in which the larger

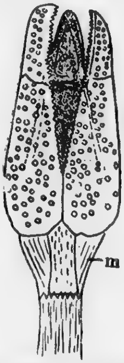

Fig. 264.—Pedicellaria from *Dorocidaris papillata* (after Koehler). *m* = muscle-fibres.

spines are somewhat enlarged towards the tip, the enlargement containing a poison-gland whose secretion is injected into the wound produced by the spine. Pedicellariæ, which have already been noted as occurring in the Asteroidea and the Euryalid Ophiuroidea, are richly developed in the Echinoids, more especially in the neighborhood of the mouth and anus. They assume varying forms, in the typical one (Fig. 264) being composed of a stalk surmounted by three calcareous pieces or teeth, hinged upon the stalk, and capable of being divaricated and approximated by means of muscles. Each tooth bears cushionlike elevations which are tactile in function, so that the three teeth are vigorously approximated when touched by any foreign body. In some pedicellariæ the teeth are very much reduced in size, but in their place three mucous glands are developed, structures sometimes found also in association with well-developed teeth. The functions of the pedicellariæ may be various; they may serve for the prehension of prey or for protection, and they have also been seen to remove excreta from the surface of the test in the neighborhood of the anus. In the bilateral Echinoids a third form of spine is found, of small size and covered by a richly-ciliated epidermis. These *clavulæ*, as they are termed, are usually associated together in groups of considerable extent termed *semites* or *fascioles*, occurring especially in the neighborhood of the plates perforated for the emission of tube-feet (Fig. 263), and in the vicinity of the anus. The clavulæ have a rich supply of nerve-fibres, and are on this account supposed to be sensory in function, though they may also assist in renewing the water in the vicinity of the tube-feet, which probably assist to a greater or less extent in respiration. A fourth variety of appendage to the test is formed by the *sphæridia*, which consist of a stalk surmounted by an oval mass of carbonate of lime traversed in all directions by delicate canals. These organs, which are usually quite small, are situated in the vicinity of the ambulacral pores or near the mouth, and are supposed to have a sensory, perhaps olfactory, function.

Owing to the presence of the firm test the muscular system is but feebly developed, being represented by the muscles attached to the spines, pedicellariæ, etc., and by those which move the parts of the masticatory apparatus when it is present.

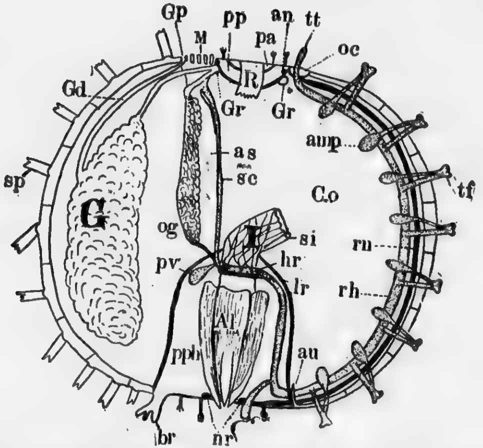

FIG. 265.—DIAGRAM SHOWING THE STRUCTURE OF AN ECHINOID.

Al = Aristotle's lantern.
amp = ampulla.
an = aboral nerve-ring.
as = axial sinus.
au = auricula.
br = external branchia.
Co = cœlom.
G = reproductive organ.
Gd = genital duct.
Gp = genital pore.
Gr = genital rachis.
hr = hydrocœl-ring.
I = œsophagus.
lr = lacunar ring.
M = madreporite.
nr = epithelial nerve-ring.
oc = ocular plate.
og = ovoid gland.
pa = perianal space.
pp = periproctal space.
pph = peripharyngeal space.
pv = Polian vesicle.
R = rectum.
rh = radial hydrocœl-vessel.
rn = radial nerve.
sc = stone canal.
si = siphon.
sp = spine.
tf = tube-foot.
tt = terminal tentacle.

The cœlom (Fig. 265, *Co*) is comparatively spacious, though traversed in some forms by the calcareous pillars already mentioned, as well as by a perforated mesentery extending from the inner surface of the test to the intestine and following the convolutions of the latter. In the bilateral Echinoids, which as a rule swallow large quantities of sand, the mesentery is much stronger than in other forms, and additional mesenterial bands are added to assist in the support of the intestine. As in the Ophiuroids, a circular partition extends from the œsophagus outwards to be inserted into the test in the neighborhood of the auriculæ, enclosing a peripharyngeal space (Fig. 265, *pph*), which has no communication with the rest of the cœlom, and contains the organs of mastication when these are present. In many forms the partition is pouched out into five radial diverticula which project into the general cœlom and are known as the *organs of Stewart* or as internal branchiæ. In those radial Echinoids in which these structures are absent, ten lobed diverticula of the floor of the peripharyngeal space project upon the outside of the body at the margin of the peristome, a pair being situated in each interambulacral region; these are termed external branchiæ (*br*). At the aboral surface of the body in the radial forms a partition similar to that enclosing the peripharyngeal space is found, surrounding the terminal portion of the intestine and enclosing a subperiproctal cavity (*pp*), while within this occurs a second partition shutting off a perianal space (*pa*). Muscular fibres occur in these partitions, and it has been suggested that by contracting and thus compressing the fluid contained in the spaces they serve to close the lumen of the rectum and the anus.

As regards the axial sinus (*as*) the Echinoids resemble the Asteroids and Ophiuroids in that the portion of the cœlom into which the larval stone-canal opens persists in the adult and forms a pouch extending downwards towards the oral surface parallel to the stone-canal, the ovoid gland (*og*) developing in its walls. Into the upper portion of it the adult stone-canal (*sc*) opens, and it communicates with the exterior through the madreporiform tubercle (*M*).

The so-called blood-vessels are, as in the Ophiuroidea, portions of the lacunar system, and are contained in perihæmal canals, as the radial schizocœlic sinuses have been termed in this group, as in the Ophiurids. These canals consist of five tubes lying between the radial hydrocœl-canals and the radial nerve-cords, and terminating blindly at their oral extremities by coming into contact with the peripharyngeal partition; they are not continued within the partition and there is no circumoral sinus. The lacunar system consists of five radial lacunæ, lying in the perihæmal canals, penetrating into the peripharyngeal space, where they unite into a circular circumoral lacuna (*lr*), from which branches pass to the walls of the digestive tract and which is in connection with the lacunæ of the ovoid gland. This structure, as stated, lies in the wall of the axial sinus, and, as in other forms, stands in close relationship to the reproductive organs, its lacunæ being continued into the walls of the genital cords.

The hydrocœl has the usual arrangement of a periœsophageal circular canal (*hr*) from which five radial canals pass off (*rh*), each terminating in a tentacle (*tt*) perforating an ocular plate. From the periœsophageal ring the stone-canal (*sc*) passes aborally to open into the axial sinus close to the madreporiform tubercle, and in addition in the radial Echinoids the ring has attached to it in each interradius a spongy structure which is usually termed a Polian vesicle (*pv*), though these structures in other groups are saclike. The tube-feet (*tf*) which perforate the ambulacral plates are in the majority of forms, and especially in the radial ones, very extensible and provided at the tip with a sucking-disk, and so assist the spines in locomotion. Two pores as a rule exist for each foot; through one of these the branch issuing from the radial canal passes, and through the other a branch passes back from the foot into the interior of the body to terminate in a saclike ampulla. The feet, however, near the aboral surface are frequently branched and lack a sucker, serving a respiratory function rather than a locomotor, and in the bilateral Echinoids, in which frequently the tube-feet occur only on the aboral surface of the test, nearly all the feet may assume a tentaclelike or pinnate form and become respiratory.

The digestive tract in all those forms in which the mouth occupies the centre of the oral surface is provided with a pharynx surrounded by a complicated calcareous masticatory apparatus usually termed *Aristotle's lantern* (Fig. 265, *Al*, and Fig. 266). When most highly developed it has the form of a pentagonal pyramid, whose apex is directed towards the mouth and consists of five similar portions united together. Each portion contains an elongated ribbonlike tooth (Fig. 266, *t*) lying in an interradius and projecting slightly beyond the lips of the mouth, though for the greater portion of its length imbedded in a calcareous socket or alveolus (*a*) composed of a right and a left half united above by epiphyses (*e*). Between each pair of alveoli, at their basal ends is another calcareous piece termed a radius, and below each of these, i.e. on its oral surfaces, lies another piece, the radula (*r*). Muscles pass to this complicated apparatus from the auriculæ and from one piece to the other, producing approximation and divarication of the projecting tips of the teeth. The presence of this apparatus brings it about that the circumoral hydrocœl and lacunar rings are forced back some distance from the mouth, surrounding the œsophagus just where it leaves the lantern. It seems well accordingly to speak of these rings as being periœsophageal rather than circumoral.

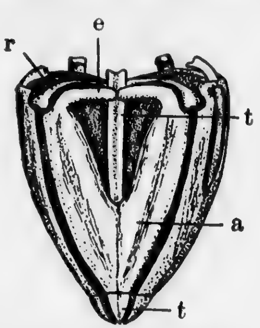

FIG. 266.—ARISTOTLE'S LANTERN FROM *Arbacia*.

a = alveolus.
e = epiphysis.
r = radula.
t = tooth.

On leaving the lantern the digestive tract, starting in the interradius *DE*, passes around the cœlomic cavity in the direction of the hands of a watch, until it reaches the interradius *CD*, when it bends abruptly on itself and, on another plane, nearer the aboral surface, retraces its course almost to its point of starting, whence it passes to the anus. The portion of the intestine immediately succeeding the pharynx is termed the œsophagus and is succeeded by a slightly wider intestine, the junction of the two parts being in some forms further indicated by the occurrence at that point of a large cœcum. As a rule, however, appendages to the digestive tract are rare, the only one occurring with any marked degree of constancy being the *siphon* (Fig. 265, *si*), a tube which arises from the œsophagus and runs, closely applied to the intestine, to open again into it at the extremity of the oral coil. The function of this structure appears to be respiratory, but it is to be noted that it is wanting in all the members of one of the orders (the *Clypeastroidea*) into which the group may be divided.

The epithelial nervous system has the usual arrangement consisting of a periœsophageal ring (Fig. 265, *nr*) and five radial cords (*rn*). As in the Ophiuroidea, these latter structures have withdrawn themselves from the ectoderm and sunk within the body-cavity, and accordingly there is to be found an epineural sinus lying below the nerve-cords. Below the nerve-ring, however, no sinus is to be found, and it seems possible that it may have fused with the peripharyngeal space. The extremity of each radial cord fuses with the ectoderm in passing through the pore in the ocular plate, and is distributed to the walls of the terminal tentacle. A muscular nervous system is present, consisting of five masses lying on the aboral surface of the radial nerve-cords just where they join the ring, and apparently having no direct connection with each other; they send fibres to the muscles of the masticatory apparatus, and are said to be wanting in those forms which lack this organ. The visceral system consists of a ring (*an*) lying near the margin of the subperiproctal cavity and imbedded in its wall. From the ring five branches arise which pass to the walls of the ducts of the reproductive organs.

Sense organs of various kinds have already been referred to, such as the terminal tentacles of the hydrocœl canals, the fascioles, and the sphæridia. In addition to these, pigment-spots occurring on the ocular plates have been regarded as eyes, and somewhat complicated structures of a bright blue color which occur abundantly over the surface of the test in a species of *Diadema* have also been regarded as light-percipient organs.

As in other forms, the reproductive system consists of the genital cords and the reproductive organs. The former have their origin from a single cord, which is a hollow tube lined internally by immature germ-cells and is connected at its oral extremity with the ovoid gland. It passes thence to the aboral surface of the body, where it forms a ring (Fig. 266, *gr*) from which in each interradius a branch passes outwards to expand into a highly racemose sac, the reproductive organ (*G*). In some forms the number of the organs may be reduced to four or even to two, though five is to be regarded as the typical number. Each organ opens to the exterior by a special duct (*Gd*), usually opening on a genital plate, but sometimes in an interradius outside the genital plates.

As already noted, there is considerable variety in the relative positions occupied by the mouth and anus, and many differences of structure are associated with these variations. It is possible, in fact, to divide the Echinoidea into three orders, which are marked out by the positions of the openings of the digestive tract.

1. Order **Desmosticha.**

In these forms the mouth occupies the centre of the oral surface, and the anus approximately that of the aboral surface, the radial symmetry usual among Echinoderms being well marked. The body is usually more or less spherical in form, though occasionally somewhat flattened; all the ambulacral plates are perforated for the emission of tube-feet, and all five ambulacral areas are equally developed (Fig. 262). In the members of this order, consequently, the bilaterality is marked externally only by the position of the madreporiform tubercle.

The primary ambulacral plates frequently fuse to form secondary plates each of which is perforated by several pairs of pores, as many as six occurring on some plates in *Strongylocentrotus*. The spines are sometimes exceedingly long, as in *Diadema*, and are usually well developed, being in *Arbacia* equal in length to about half the diameter of the body. The auriculæ are the only representatives of the calcareous plates or bars which extend from the oral to the aboral surface, and an Aristotle's lantern is always well developed, its alveoli being much longer than broad. In this order external branchiæ are generally present, the genus *Cidaris* and its allies alone lacking them and possessing Stewart's organs. It is customary, therefore, to divide the order into two sub-groups: the Entobranchiata, including the *Cidaridæ*, and the Ectobranchiata, including all other forms, such as *Strongylocentrotus* and *Arbacia*.

2. Order **Clypeastroidea.**

In this order, named from one of the genera contained in it, the mouth still occupies the centre of the oral pole, but the anus is situated in the interradius *AB*, either at the margin of the flattened test, as in *Echinarachnius* (Fig. 267), or on its oral surface, as in *Mellita*. In *Clypeaster* the body is but slightly flattened, but in the two other genera already mentioned the flattening is carried to such an extent that the test has a more or less disklike shape, whence the term Sand-dollars applied to certain forms.

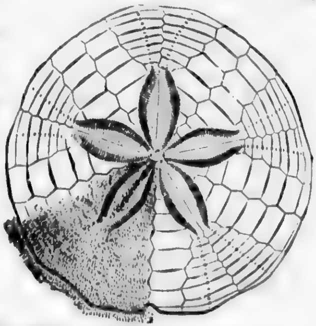

Fig. 267.—A Clypeastroid Echinoid, *Echinarachnius parma*, from the Aboral Surface with the Spines for the most part removed (after A. Agassiz).

In accordance with the shifting of the anus from the centre of the apical system certain changes take place in it, the most marked being an extension of the madreporiform tubercle until it includes all the genital and ocular plates, the genital pores being forced outwards so as to lie on one of the interambulacral plates, and in some cases the pore of the posterior interradius *AB* and the corresponding reproductive organ is wanting (*Echinarachnius*). The perforated ambulacral plates are as a rule confined to the apical portion of the aboral surface, the plates near the margin of the test and those upon the oral surface being imperforate. The perforated plates are of course very narrow at the apical end of the series, and gradually enlarge as they pass towards the edge of the test, giving thus the appearance of five flower-petals, and hence the ambulacra or areas occupied by perforated plates are termed petaloid. In *Echinarachnius*, for instance, the plates after having reached their greatest width retain it to their abrupt termination (Fig. 267), the petals being then termed open, but in other forms, e.g. *Mellita*, they contract again peripherally, in which case the ambulacra are said to be closed.

The pores belonging to each pair are generally united by a groove, and are termed yoked pores, and in *Mellita*, for example, in addition to the pair of yoked pores on each plate there is a third one situated near the middle line of the ambulacrum. The tube-feet which project from the yoked pores are frequently pinnate in form, while those emitted through the single pores are simple and tentaclelike. The spines are generally very small, though those of the oral surface serve for locomotion.

In *Mellita*, towards the periphery of the test, the imperforate ambulacral plates of the radii *A*, *B*, *C*, and *E* do not meet, leaving elongated holes passing through the test, and the same thing also occurs with the plates in the interradius *AB*, so that altogether five such holes exist. In other forms, instead of holes, notches occur at the margin of the test, and other interambulacra than that in which the hole occurs in *Mellita* may be affected. Calcareous columns extend from the oral to the aboral surfaces of the test, being especially abundant towards the periphery, and calcareous plates uniting the two surfaces occur on either side of each ambulacrum. An Aristotle's lantern is present, but the alveoli are usually broader than long.

3. Order **Petalosticha.**

In this order, as its name indicates, the ambulacra are usually petaloid, and the bilaterality indicated in the Clypeastroids is more pronounced, since neither the mouth nor the anus retains its original position at the centre of the oral or apical surface. The anus lies in the posterior interradius *AB*, while the mouth has moved forwards to a greater or less extent along the radius *D*. The test is oval or, frequently, somewhat heart-shaped, owing to the anterior radius *D* being more or less depressed so as to form a groove (Fig. 263).

The madreporiform tubercle extends usually through the centre of the apical system into the posterior interradius, thus dividing the apical system. The posterior genital pore is obliterated in all members of the order, and the reproductive gland corresponding to it disappears, so that but four reproductive organs and pores are present (*Spatangus*). In some forms, however, the reduction of the reproductive organs and pores is carried still further by their disappearance in the right anterior interradius *CD*, and those of the left anterior interradius *DE* may also disappear, the genital plate becoming part of the madreporiform tubercle, so that the number of reproductive organs and genital pores may be reduced to two (*Moira*). The ambulacra are usually dissimilar, especially in heart-shaped forms, in which the anterior ambulacrum becomes much modified. Fascioles are generally present, arranged in different manners in different species, in some surrounding the ambulacra, in others forming a ring in the vicinity of the anus, and in others arranged in numerous patches or lines. Spines are abundantly present and are usually of a moderate length. The mouth is bounded behind by a well-marked lip or labrum, produced by the extension forwards below the mouth-opening of the plates of the posterior interambulacrum *AB*. There is no Aristotle's lantern in the Petalosticha.

Development of the Echinoidea.—The development is in its general features very similar to that of the Ophiuroids, the free-swimming larvæ having a closely-similar form and being known by the same name. The Echinoid Pluteus (Fig. 261) may, however, in some cases be distinguished by the occurrence of two (*Arbacia*) or three (*Spatangus*) processes upon the posterior portion of the body, which are wanting in the Ophiurid larvæ; and furthermore in some Echinoid Plutei (*Arbacia*) two earlike lobes fringed with cilia occur upon the sides of the posterior portion of the body and are known as ciliated epaulettes. The young Sea-urchin develops in the posterior portion of the body of the larva as in other forms, the armlike processes and the præoral lobe of the larval body being gradually resorbed.

The relationships of the various groups have already been referred to and need not be again discussed here, except to repeat the statement that the evidence at our disposal indicates that the Desmosticha are the most primitive, while the Clypeastroidea and Petalosticha are secondarily-derived forms. The bilaterality of these latter forms is not to be regarded, therefore, as having any phylogenetic significance.

Class V. **Holothuroidea.**

The Holothurians (Fig. 268) are characterized so far as their form is concerned by being elongated in the oral-aboral axis, having thus a somewhat wormlike form, the mouth being at or near one extremity and the anus at the other, except in the genus *Rhopalodina*, in which the two openings are approximated. As a rule the body is cylindrical, but in some forms, such as *Psolus* and the *Elasipoda*, there is a well-marked flattened ventral surface. Three of the radial hydrocœl-canals lie upon this ventral surface, the other two being dorsal, and it is usual to apply the term trivium to the ventral radii and bivium to the dorsal. It must be recognized, however, that this use of the terms does not imply a homology with the radii similarly named in the Echinoidea, since in the latter the radii *C*, *D*, and *E* constitute the trivium, whereas in the Holothurians it is the radii *A*, *B*, and *E*.

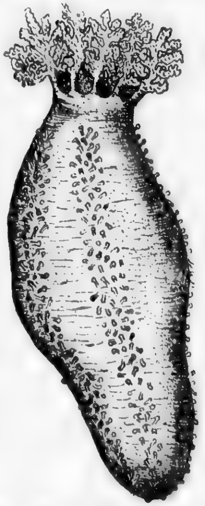

Fig. 268.—*Pentacta frondosa*, a Holothurian.

The mouth is surrounded by a circle of tentacles varying in number from ten to thirty. There are at first five primary tentacles, interradial in position, which are formed in connection with five cæcal outgrowths of the hydrocœl-ring, and the tentacles subsequently formed receive branches from the five primary cæca. In shape the tentacles vary considerably, being cylindrical in some forms, arborescent or pinnate in others (Fig. 268), and in others peltate, and in some forms they are retractile.

The exterior of the body is usually covered by an epithelium over which a cuticle may be developed, but in some forms the ectodermal cells sink into and become fused with the subjacent connective tissue. The calcareous skeleton is but feebly developed in the Holothurians, the body-walls having as a rule a somewhat leathery consistency, though in *Elpidia* interlocking spicules, and in *Deima* and *Psolus* closely-approximated or overlapping plates, give the skin considerable rigidity. In the majority of forms, however, the calcareous skeleton is represented by scattered plates of various shapes, perforated, knobbed, sometimes wheel-shaped as in *Chirodota*, or associated with an anchorlike spicules in *Synapta*, and are not sufficiently numerous to give rigidity to the integument, which in *Synapta* may even be thin and translucent. There is no indication of an apical system of plates, though in *Mülleria* a circle of five plates surrounds the anus, but the oral system is represented in a species of *Psolus* by five plates which may be closed over the mouth and tentacles. In other parts of the body than the integument calcareous matter is also frequently deposited, especially in the connective tissue of the wall of the peripharyngeal cavity, the pharyngeal ring (Fig. 269, *b*) so formed consisting typically of five radial ossicles, grooved or perforated by the radial nerves and hydrocœl-canals, and of five interradial ossicles alternating with them, though in those forms in which the number of tentacles is greater than ten the number of the interradial ossicles may be increased. Spicules are also found in the mesentery, and in some forms plates or a calcareous network develops in the wall of the pharynx. Spines are rarely present, though the plates of *Echinocucumis*, *Elpidia*, and a few other forms bear them, and pedicellariæ are entirely wanting.

The cœlom is traversed by several mesenteries uniting the digestive tract to the body-wall, the most constant being the so-called dorsal mesentery (Fig. 269, *m*), which lies in the anterior portion of the interradius *CD*. The portion of the cœlom which surrounds the œsophagus is separated from the rest, as in the Echinoidea, and forms the peripharyngeal space, and similarly in some forms (*Cucumaria*, *Holothuria*) a perianal space surrounds the terminal portion of the digestive tract. In *Synapta* and its allies there are attached by slender peduncles to the body-wall along the line of the mesenteries, and hanging freely in the body-cavity, numerous ciliated urnlike bodies, which probably function similarly to the ciliated cups of the Crinoids in maintaining a circulation of the cœlomic fluid.

So far as is known, the portion of the cœlom which in the embryo opens to the exterior by the water-pore and with which the stone-canal communicates in the Asteroids and Echinoids does not persist in the adult Holothurian, and consequently there is no axial sinus, and it is doubtful if a structure comparable to the ovoid gland of other forms exists. Schizocœlic sinuses corresponding to the perihæmal canals of the Echinoids occur in their usual position between the nervous system and the hydrocœl-canals, and consist of a ring accompanying the nerve-ring and five radial canals which abut against the ring at their oral ends but seem to be completely separated from it by septa. A lacunar system is well developed, consisting of a plexus in the walls of the intestine, the various branches uniting to form a dorsal and a ventral intestinal vessel, which, passing forwards, unite with a lacunar ring surrounding the œsophagus at about the level of the hydrocœl-ring. From this ring five radial lacunæ extend backwards, lying in the connective tissue between the radial perihæmal sinus and the hydrocœl-canals, and giving branches to the tentacles and the tube-feet. A lacuna also extends from the periœsophageal lacunar ring to the reproductive organs arising from a thickened portion of the ring, and this thickening has been regarded as the rudiment of the ovoid gland.

The hydrocœl has the usual arrangement, consisting of a ring (Fig. 269, *c*) surrounding the œsophagus behind the ring of peripharyngeal ossicles, and having arising from it a stone-canal which in the majority of forms hangs freely in the cœlomic cavity, where it terminates in a madreporiform plate. In the embryo it as usual opens upon the surface of the body, and this condition is retained in many *Elasipoda*, in which the canal opens upon the dorsal surface of the body, probably indirectly through the intervention of an ampulla, as in other forms. In the majority of forms, however, the connection with the exterior becomes lost, the ampulla which is present in the embryo disappearing, and occasionally a number of secondary canals develop. A single Polian vesicle (*e*) is usually attached to the ring, but in some cases the number of these structures may be considerably increased. Five interradial canals arise from the ring and pass forwards to the tentacles, branching if these structures are more than five, and in some forms (*Holothuria, Chirodota*) these tentacular canals are provided with ampullæ. Five radial canals also pass backwards from the ring in all forms except the Synaptidæ, corresponding to the radial hydrocœl-canals of other Echinoderms and bearing tube-feet.

The distribution of these latter structures is peculiar in many forms. In *Molpadia* although the canals are present the tube-feet are entirely wanting, as they are also from the dorsal canals of *Psolus* and from the median canal of the trivium of the Elasipoda; when present they may be arranged along the lines of the radial canals (*Cucumaria, Pentacta*, Fig. 268) or may be scattered irregularly over the surface of the body (*Thyone*). In form they also vary considerably, being either simple fingerlike processes or else tipped with a sucker. Frequently the tube-feet are not retractile, and in the Elasipoda they take the form of strong well-developed conical processes arranged in pairs.

Owing to the absence of a firm test in the Holothurians there is a much more extensive development of the muscular system than in other Echinoderms. The inner surface of the body-wall is formed by a layer of circular muscle-fibres, and on each side of each radial hydrocœl-canal is a longitudinal muscle-bundle (Fig. 269, *p*) from which in some forms special bundles pass to the peripharyngeal ossicles and serve as retractors of the tentacles and mouth-disk.

As stated the mouth is usually at the anterior end of the body at the centre of a disk surrounded by the tentacles, but in the Elasipoda it has a somewhat ventral position. The digestive tract is a simple tube, which occasionally has a perfectly straight course from mouth to anus, but more frequently it is bent twice upon itself, so that there is an anterior descending limb (Fig. 269, *f*), an ascending (*g*), and a posterior descending one (*h*). The terminal portion of the posterior descending limb is dilated, forming a cloaca (*i*) from whose wall muscle-bands (*q*) radiate to the walls of the body. This cloaca is rhythmically contractile, and has opening into it except in the Synaptidæ two much-branched structures termed the respiratory trees (*k*). As their name indicates, these structures are supposed to have a respiratory function, but it is possible that they may also aid in excretion, the waste products of metabolism collecting in the cells lining the interior of the tubular branches and being carried to the exterior by a desquamation of the cells. In addition in a small number of forms (*Holothuria*) there occur upon one side of the cloaca a large number of slender tubes (*l*), which, at the will of the animal, can be evaginated so as to project through the anal opening. These constitute the organ of Cuvier, the function of which is not as yet satisfactorily explained.

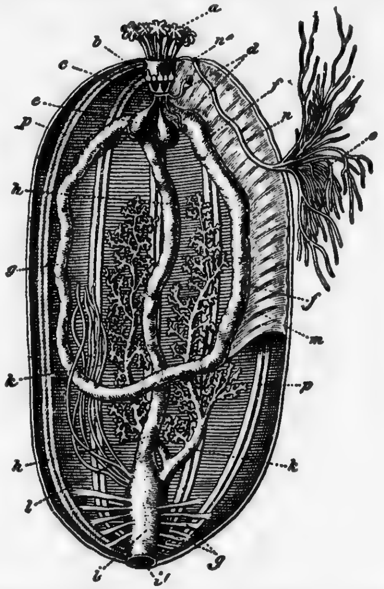

FIG. 269.—DIAGRAM REPRESENTING THE INTERNAL ANATO LOTHURIAN (after LUDWIG from LEUNIS).

a = tentacles.
b = calcareous pharyngeal ring.
c = hydrocœl-ring.
d = stone-canals.
e = Polian vesicle.
f, g, h = intestine.
i = cloaca.
i' = cloacal opening.
k = respiratory trees.
l = Cuvierian organ.
m = dorsal mesentery.
n = duct of reproductive organ.
o = reproductive organ.
p = longitudinal muscles.
q = radiating muscles of the cloaca.

The epidermal nervous system consists of a periœsophageal ring and five radial nerves as in other forms, and in addition five interradial nerves pass from the ring to the tentacles. The system is almost completely separated from the ectoderm, with which in the embryo it is connected, and lies within the tissues of the body, the radial nerves only at their posterior extremities passing through the tissues of the body-wall to fuse with the ectoderm. In accordance with this arrangement an epineural sinus accompanies each radial nerve, though absent from the periœsophageal ring. The muscular nervous system has an arrangement similar to that of the sinuses, being well defined in connection with the radial nerves, though wanting in the periœsophageal ring. No trace of the aboral nervous system has been discovered in the Holothurians.

The tentacles serve as tactile organs, and may have also an olfactory function in addition to being respiratory, and in the Synaptids numerous ciliated depressions with a strong nerve-supply are found upon them. No visual organs occur in the Holothurians, but in the Synaptids and Elasipoda otocysts occur. In *Synapta* there are ten of these organs, imbedded in the connective tissue in the neighborhood of the periœsophageal nerve-ring, one lying on each side of each radial nerve close to its origin from the ring. Each otocyst contains a number of otoliths, and is lined interiorly by cells which are provided with cilia. In *Elpidia* the number of otocysts is fourteen and in other Elasipoda the number may be much greater, amounting to about thirty-six in a species of *Kolga*.

The Synaptids and Molpadids are hermaphrodite, but all other Holothurians are bisexual. The reproductive organs (Fig. 269, *o*) consist of one, or in some cases two bundles of cæcal tubes which are attached to the left side (or on both sides) of the dorsal mesentery, and open by usually a single duct (*n*) upon the dorsal median line, sometimes within the circle of tentacles, but usually behind it. The cæca are lined interiorly with an epithelium from which the ova and spermatozoa develop.

The arrangement of the reproductive organs in the Holothurians is decidedly different from what occurs in other groups of Echinoderms, and the differences are associated with the absence or reduction of the ovoid gland and of an aboral nervous system. The number of the organs is very much reduced, and no genital cords have as yet been discovered. It is interesting to note, however, the existence of a genital lacuna mentioned above, in association with which the reproductive organs seem to develop, and it may be, as stated, that the lacunar thickening from which it arises is to be regarded as representing the ovoid gland, which, as has been seen, is intimately connected with the lacunar system in other forms. It seems probable that in harmony with the shortening of the stone-canal and its separation from the body-wall, and with the abortion of the axial enterocœl, there has been a shortening of the genital cords so that the aboral ring no longer exists, and the reproductive organs, reduced in number, develop directly upon the wall of the genital lacuna. It must be remarked that in some forms there is no distinct genital lacuna, but the reproductive organs are associated with the intestinal lacunæ, a condition which may be secondary.

Development of the Holothuroidea.—The typical larva of the Holothurians is known as the *Auricularia* (Fig. 270), and is distinguished from that of the Asteroids, Ophiuroids, and Echinoids by being destitute of armlike processes. In later stages the ciliated bands fuse in such a manner as to form a series of circular bands surrounding the barrel-shaped larva and recalling the larva of the Crinoids. By the gradual elongation of this larva and the disappearance of the ciliated bands the adult form is acquired, there being no absorption of any extensive portion of the larval body as in the Brachiolaria and Pluteus.

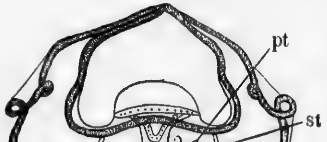

FIG. 270.—**AURICULARIA LARVA OF** *Synapta* (after SEMON).
dp = dorsal pore.
H = hydrocœl.
pt = primary tentacles.
st = secondary tentacles.

The Phylogeny of the Echinoderma.—The Echinoderms form a well-defined group showing little indication of affinities with other forms, and the establishment of a plausible phylogeny is an unusually difficult task. One thing, however, seems certain from their developmental history, and that is that they have been derived from primitive bilateral forms, and that the radiality characteristic of the adults has been secondarily acquired. The larvæ are strictly bilateral, there being indications that originally two water-pores, situated symmetrically upon the dorsal surface, existed. The first question to be decided then is the cause of the radial symmetry seen in the adult.

Bilaterality in the animal kingdom is usually associated with an antero-posterior differentiation, and this with a definite axis of progression. Thus in an Annelid the most anterior metamere is that which is apt to first come into contact with new conditions of environment, and consequently it has become specially provided with sense-organs for the perception of these new conditions whether favorable or unfavorable; similarly the conditions affecting the dorsal and ventral surfaces are different and consequently a dorso-ventral differentiation exists; while on the other hand the conditions affecting the two sides of the body are apt to be alike, and consequently the differentiations which occur on each side of the median line are usually alike. Bilaterality is then associated with a free-mode of life.

Conversely, radiality is usually associated with indefinite axes of progression or with a fixed mode of life, and the idea suggests itself that the radiality of the Echinoderms may be the result of a fixation of the bilateral larva. The majority of recent Echinoderms are, it is true, free forms, the Crinoids alone being sessile, but it will be found that geologically the free forms are the latest to appear, and that the Pelmatozoa are especially characteristic of the Palœozoic rocks. This would imply that the Crinoids are to be regarded as the most perfect representatives among recent forms of the ancestral types, an idea which is borne out by certain points in Echinoderm development. Thus the calyx of the Crinoid is developed in the posterior portion of the oval larva, the anterior portion being occupied by the stalk; in the Brachiolaria and Pluteus larvæ the adult body is developed in the posterior portion of the larva, the anterior portion undergoing absorption, an arrangement which may be explained by supposing that originally the adult forms which possess these larvæ were stalked, but secondarily acquired a free mode of life, and that as a result the stalk disappeared, the body, corresponding to the calyx of the Crinoid, still developing in its accustomed position in the posterior portion of the larva. In the Holothurians there is not apparently that distinction into anterior and posterior regions in the larva which obtains in other forms, but it is to be noted that in the young *Cucumaria*, for example, there is a well-marked præoral lobe which later on disappears and may represent the partially-aborted stalk region of other forms.

Attempts have been made to trace out a phylogeny taking the Holothurians as a primitive type and tracing them back to such forms as the Gephyrean worms, the presence of respiratory trees in both forms suggesting a possible affinity. Or again the later barrel-shaped larva with five tentacles has been considered to represent a common ancestor for all the various groups of Echinoderms, the term *Pentactæa* being given to the hypothetical ancestor. Neither of these views, however, affords any clue to the origin of the radiality, and the structure of the Holothurians departs so widely from that of the other groups that it seems preferable to consider them as most remote from the common ancestor. Furthermore as regards the *Pentactæa* it is difficult to understand how there should be so much similarity in structure of the different forms if they all differentiated independently from this common ancestor.

From the evidence at our disposal it seems far more logical to accept a stalked form for an ancestor, and to consider the Crinoids as approaching it more nearly than any other recent forms. It has been suggested, with no little reason, that the Cystoidea were the ancestors of the Crinoids and perhaps of most of the other groups as well. A full consideration of this point, as well as of the details of the conversion of the bilateral remote ancestor into the radial form, would carry us beyond the scope of this work, and reference must be had to special works treating of these questions (P. and F. Sarasin, O. Bütschli).

As stated, the relationships of the Echinoderms to other groups is a question which has not yet been satisfactorily settled. Attention may be called, however, to the remarkable similarity of the *Tornaria*-larva of *Balanoglossus* (p. 606) to the Echinoderm larva, a similarity so great as to suggest affinity. This suggestion may, however, be postponed until the *Tornaria* has been described.

SUBKINGDOM METAZOA.

TYPE ECHINODERMA.

I. Class CRINOIDEA.—Usually stalked; with ten (or five) arms, provided with lateral pinnules, arising from the margin of the cup-shaped body. Dermal skeleton well developed.
  - In adult life free-swimming. *Antedon*, *Actinometra.*
  - Fixed throughout life, stalk with numerous whorls of cirri. *Pentacrinus.*
  - Fixed throughout life, slender stalk with cirri either wanting or only on distal joints. *Rhizocrinus*, *Calamocrinus*, *Hyocrinus*, *Thaumatocrinus.*
  - Fixed throughout life, stalk short and stout. *Holopus.*

II. Class ASTEROIDEA.—Free forms; stellate or pentagonal in shape; arms containing cæcal processes of digestive tract; ambulacra limited to oral surfaces.
  - Dermal skeleton reticulate; no paxillæ; anus present. *Asterias*, *Brisinga*, *Asterina*, *Zoroaster.*
  - Dermal skeleton of separate plates; paxillæ present; no anus. *Astropecten*, *Luidia.*

III. Class OPHIUROIDEA.—Free forms; stellate in shape; arms not containing cæcal processes of the digestive tract; ambulacra limited to oral surface; ambulacral ossicles contained within the arms.
  1. Order *Ophiurida.*—Arms unbranched; madreporiform tubercle on mouth-shield. *Ophiura*, *Ophiolepis*, *Amphiura*, *Ophiactis*, *Ophiothrix*, *Ophioderma*, *Ophiomyxa.*
  2. Order *Euryalida.*—Arms usually branched; mouth-shields not well developed; usually several madreporiform tubercles. *Astrophyton*, *Trichaster.*

IV. Class ECHINOIDEA.—Free forms; without arms; test composed of twenty rows of plates; ambulacra extending from oral to aboral surfaces or else limited to aboral surface.

1. Order *Desmosticha.*—Ambulacra all similar, extending from oral to aboral surfaces; mouth and anus in centre of the oral and aboral surfaces respectively; masticatory apparatus present.
   With internal branchiæ. *Cidaris.*
   With external branchiæ. *Asthenosoma*, *Salenia*, *Diadema*, *Arbacia*, *Strongylocentrotus.*
2. Order *Clypeastroidea.*—Ambulacra all similar, limited to the aboral surface; mouth in centre of oral surface, anus excentric; masticatory apparatus present. *Clypeaster*, *Echinarachnius*, *Mellita.*
3. Order *Petalosticha.*—Ambulacra more or less dissimilar, limited to the aboral surface; mouth and anus both excentric; masticatory apparatus wanting. *Moira*, *Spatangus*, *Brissopsis.*

V. Class HOLOTHUROIDEA.—Free forms; body mostly elongate and vermiform; mouth surrounded by circle of 10–30 tentacles; skeleton usually of small scattered plates.

1. Order *Elasipoda.*—Bilateral symmetry well marked; stone-canal frequently opens to exterior; no respiratory trees. *Deima*, *Elpidia.*
2. Order *Pedata.*—Bilateral symmetry as a rule not particularly well marked; respiratory trees present; stone-canal not opening to exterior; tube-feet well developed.
   Tentacles branched dendritically. *Cucumaria*, *Psolus*, *Thyone.*
   Tentacles pinnate. *Rhopalodina.*
   Tentacles peltate. *Holothuria*, *Mulleria.*
3. Order *Apoda.*—Bilateral symmetry not well marked; stone-canal not opening to exterior; tube-feet wanting.
   Respiratory trees present. *Molpadia*
   Respiratory trees wanting. *Synapta*, *Chirodota.*

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CHAPTER XVII.

TYPE PROTOCHORDATA.

THE type Protochordata contains a number of forms which present certain features of similarity to the Chordata (Vertebrata), one member of the type, *Amphioxus* being frequently considered as belonging to that group, which is to be regarded as the most highly differentiated of all the types composing the Animal Kingdom.

The various groups of the Protochordata differ greatly in general appearance, but certain structural features of great morphological importance are common to all of them. These may be briefly stated as (1) a *notochord*, consisting of a more or less well-developed rod, arising from the mid-dorsal line of the digestive tract and either extending the entire length of the body, or else limited to its anterior or its posterior part, or even present only during larval life, as in the majority of the Tunicata; (2) *branchial slits* which place the cavity of the pharynx in communication with the exterior and serve as respiratory organs; (3) *a central nervous system*, situated in the mid-dorsal line of the body, and arising in some forms as an ectodermal invagination.

Metamerism is but feebly indicated in the majority of cases, some forms possessing only three mesodermal somites, while others, such as some of the Tunicata, show traces of it only in the posterior region of the body, *Amphioxus* being the only form in which it is at all well marked. Limbs do not occur in any members of the group, nor are there any special jaws or organs of mastication. All the members of the group are marine, and the various classes possess a wide geographical distribution.

I. CLASS **HEMICHORDA.**

The members of this class are characterized by the notochord being a comparatively small diverticulum of the anterior portion of the digestive tract and containing a more or less perfect cavity which communicates with the œsophagus. The body is divisible into three regions: an anterior præoral epistome or proboscis, a median collar region, and a posterior visceral sac or trunk region. The cœlom is divided into corresponding regions, a pair of pores placing the collar compartment in communication with the exterior, while one or two additional pores perform a similar office for the epistome or proboscis cavity. The nervous system remains in connection with the ectoderm, and its principal portion is situated in the collar region.

1. Order **Pterobranchia.**

This order contains but two genera, *Rhabdopleura* and *Cephalodiscus*, the former occurring in deep water off the coast of Norway, while the latter was obtained by the "Challenger" Expedition in the Straits of Magellan.

Rhabdopleura (Fig. 271) is a colonial form, consisting of a stolonlike system of tubes ramifying over the surface of stones, etc., and giving off shorter lateral tubes each one of which contains an individual. The tubes are composed of chitinlike material and form a "house" for the colony, and

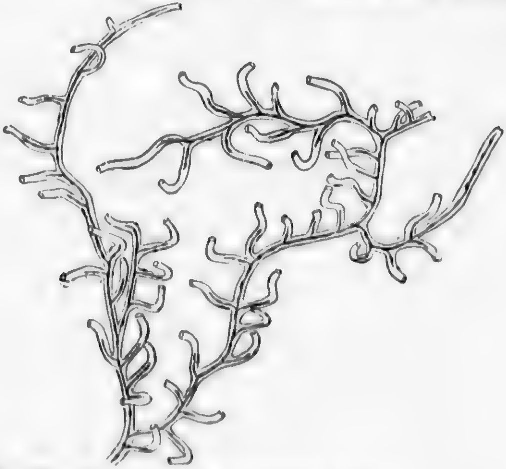


FIG. 271.—COLONY OF *Rhabdopleura* (after LANKESTER).

are traversed, except towards the extremities of the lateral tubes where the individuals occur, by a chitinous rod which results from the chitinization of what was once the stem of the various polyps. Each of these is stalked (Fig. 272), the stalk (*C*) becoming continuous below with the chitinous rod, and each consists of three well-marked regions. What may be termed the anterior portion of the body is formed by a large disklike epistome (*D*), beneath which on the ventral surface is

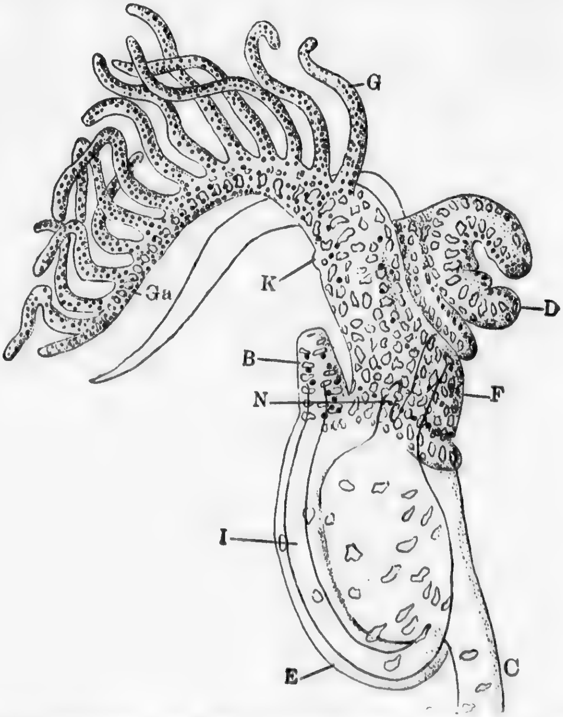


FIG. 272.—INDIVIDUAL OF *Rhabdopleura* (slightly modified after LANKESTER).
(N.B.—The tentacles of one side of one arm only are represented.)

B = anal papilla.
C = stalk.
D = epistome.
E = trunk region.
F = collar region.
G = tentacle.
Ga = arm.
I = intestine.
K = sensory papilla.
N = notochord.

the mouth. Behind these is what is termed the collar region (*F*), which bears upon its dorsal surface two long armlike processes (*Ga*), each carrying a double row of ciliated tentacles (*G*) arranged pinnately. The third region is the visceral sac (*E*), from the posterior and ventral portion of which the stalk arises, while dorsally and anteriorly it carries a stout papilla (*B*), at the extremity of which the anus opens.

The digestive tract consists of a straight œsophagus traversing the collar, and having connected with it on the dorsal surface a short blind process (*N*) whose cavity communicates with that of the œsophagus. This is the rudimentary notochord. The œsophagus opens into a large saclike stomach, from the lower end of which the intestine (*I*) arises, and, bending upon itself, runs forwards to open on the anal papilla.

The nervous system consists of a thickening of the ectoderm on the dorsal surface of the collar region, where is also found a small ciliated elevation (*K*) supposed to be sensory; no other special sense-organs occur. On each side of the collar a pore occurs which, by a short ciliated canal which perforates the wall of the body, places the cœlom of the collar in communication with the exterior, and may be regarded as representing an excretory organ. No epistome-pore or branchial slits have yet been observed.

Cephalodiscus resembles *Rhabdopleura* in being colonial, but the house is gelatinous, and the various buds formed from the short stalk do not remain in connection with each other, but early separate from the parent. Each polyp (Fig. 273) consists of three regions—an anterior præoral portion which forms a large epistome, a middle collar region, and a posterior visceral sac; the body-cavity being divided into three corresponding regions. Two epistome-pores occur, the canal leading from the cœlom to them passing through the anterior part of the nervous system (*n*). The dorsal ectoderm of the collar region is thickened to form the central nervous system, and on each side of this is a cluster of six tentacles (*t*), each ending in a knoblike dilatation and bearing numerous lateral pinnules arranged in two rows. At the sides the collar is continued backwards as a pair of lateral folds which slightly overlap the anterior portion of the visceral sac and form the *operculum*, upon the inner surface of which there is on each side a collar-pore.

The mouth (*m*) opens beneath the epistome into an œsophagus, which in the collar region bears a dorsal diverticulum, the notochord (*x*), projecting forwards into the epistome. In this same region there is on each side a branchial slit (*sp*), structures which are apparently wanting in *Rhabdopleura*. Behind the œsophagus opens into a saclike stomach from which the intestine, bending upon itself, passes forwards to open (*a*) upon the dorsal surface of the visceral sac, a short distance behind the collar.

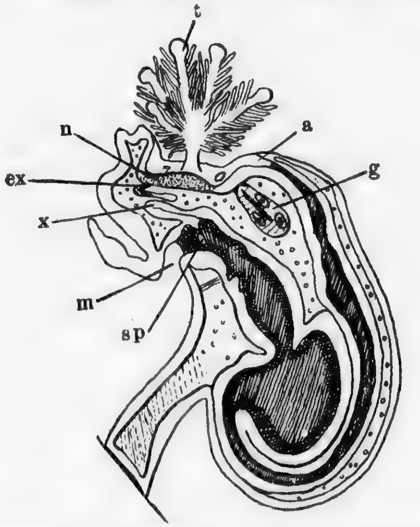


FIG. 273.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH *Cephalodiscus* (after EHLERS from KORSCHELT and HEIDER).

a = anus.
ex = excretory organ.
g = ovary.
m = mouth.
n = nervous system.
sp = branchial slit.
t = tentacles.
x = notochord.

The collar-pores probably serve as excretory organs, and it has been stated that the epistome-pores open into well-developed tubes (*ex*) terminating in the epistome cavity in a dilatation; they also have been regarded as excretory. The reproductive organs (*g*) are paired sacs, which open on the dorsal surface just in front of the anus. No circulatory system occurs in the Pterobranchia, and nothing is yet known concerning the embryonic development of either of the genera contained in the order.

2. Order **Enteropneusta.**

The order Enteropneusta contains a small number of closely-related forms which, until recently, have been grouped together in a single genus, *Balanoglossus*, and which, notwithstanding that they present in some respects a decided advance in structure over the Pterobranchia, yet may properly be associated in a class with that order.

All the species live buried in sand, and the body is elongated and vermiform, the digestive tract being practically straight and the anus terminal. The anterior portion of the body (Fig. 274, *pr*) has the form of a cylindrical proboscis, corresponding to the epistome of the Pterobranchia and united to the second region by a narrow neck, upon the dorsal surface of which is a pore (occasionally two) which places the proboscis-cœlom in communication with the exterior, while upon its ventral surface, just where it joins the second region, is the mouth.

The second region is comparatively short and forms the collar (*c*), its posterior border being prolonged backwards for a short distance in the form of a fold on each side, as in *Cephalodiscus*. These folds enclose between their inner walls and the sides of the anterior part of the third portion of the body a space which communicates behind freely with the exterior and is known as the *atrium*. The posterior or trunk region of the body is much longer than either the proboscis or collar regions, and contains the greater portion of the digestive tract and the reproductive organs. Anteriorly it is somewhat flattened and presents on the dorsal surface a ridge, on either side of which are to be found a varying number of U-shaped pores (*br*) with ciliated margins. These pores lead into short tubes opening internally into the cavity of the digestive tract and are the *branchial slits*. They seem to increase in number during the life of the animal, the posterior ones being merely circular openings, as the anterior ones are in the younger stages of development, a tonguelike valve later growing down from the dorsal border of the pore and giving it its U-shaped form. Water flows in at the mouth and passes out through the branchial slits, which thus possess a respiratory function. A few of the anterior slits open

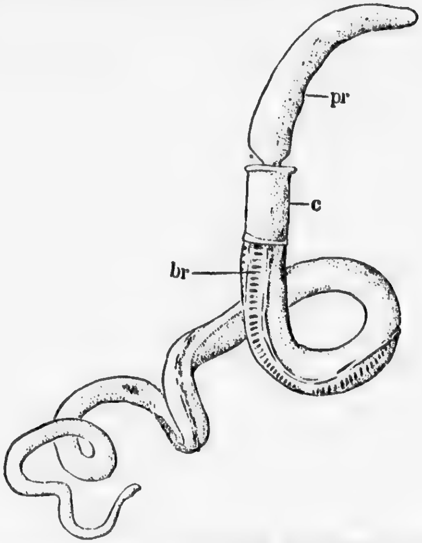


Fig. 274.—*Balanoglossus Kowalewskii* (after Minot from Spengel).
br = branchial slit. *c* = collar. *pr* = proboscis.

externally into the atrium, being covered over by the backwardly-projecting atrial folds of the collar, but the majority are quite uncovered and are plainly visible from the exterior.

The ectoderm contains numerous mucous glands and is ciliated throughout, no external cuticle or "house," such as occurs in the Pterobranchia, being developed. Below it rests upon a thin basement-membrane.

The cœlom is clearly marked out, and consists of three portions completely separated from one another and corresponding to the three body regions. The proboscis-cœlom (Fig. 275, *A*, *pc*) is, in its anterior portion, a simple unpaired cavity lined with delicate cells and traversed by circular and longitudinal (*lm*) muscle-fibres. Posteriorly it is prolonged into two horns, between which lies a mass of tissue consisting of several different organs. The centre of the mass is occupied by the notochord (*nc*), which is, as in the Pterobranchia, a forwardly-directed diverticulum of the dorsal wall of the anterior portion of the digestive tract and contains a more or less distinct cavity communicating with that of the œsophagus. Dorsal to the notochord lies a contractile heart (*h*), and dorsal to this again, and surrounding it, a sac (*ps*) containing a few, or in some cases many, cellular elements. This proboscis-vesicle, as it has been termed, may possibly represent a portion of the proboscis-cœlom, which would then consist of two separate cavities, originally right and left, one of which becomes very large and fills the greater portion of the proboscis, while the other remains quite small. Surrounding these structures are a number of folds of the splanchnic layers of the proboscis-cœlom (*pg*), loops of blood-vessels lying in the folds, while the cells covering them frequently contain yellow granules. It has been supposed that these granules indicate a glandular function for the cells, and consequently the entire mass of folds has been termed the proboscis-gland.

The cœlomic cavities of the collar (Fig. 275, *B cop*) and trunk are much simpler and are paired, the cavities of the right and left sides being separated from each other by dorsal and ventral mesenteries. From the dorsal portion of the anterior end of the trunk-cœlom two prolongations extend forward into the collar, lying on each side of the dorsal blood-vessel and forming the perihæmal cavities in the interior of which are longitudinal muscle-fibres. Two other similar forward prolongation of the trunk-cœlom lie between the collar cœlom and the œsophagus, forming the peripharyngeal cavities.

In contradistinction to what occurs in the Pterobranchia, a well-developed blood system is present, consisting in the collar and trunk of a dorsal and ventral longitudinal vessel with distinct muscular walls and lying in the mesenteries. From the dorsal vessel branches pass to the tonguelike process of the branchial slits, and the vessel itself is continued forward into the proboscis to enter a space between the proboscis-vesicle and the notochord which is termed the heart.

The blood-spaces in the proboscis-gland communicate with the heart, and the dorsal and ventral vessels of the collar and trunk are united by a double set of fine lacunar capillaries, one set being situated in the body-wall, and the other in the wall of the intestine. The blood is a colorless coagulable fluid, apparently destitute of corpuscles.

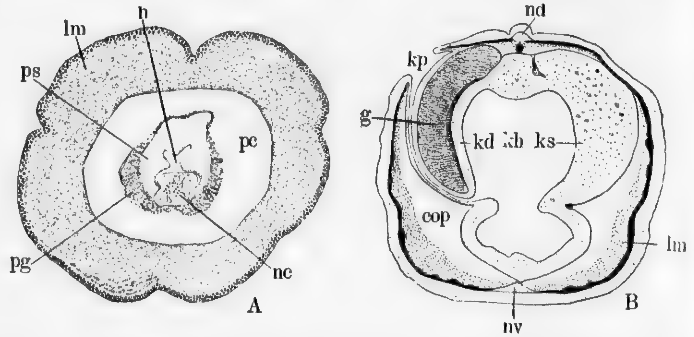


FIG. 275.—TRANSVERSE SECTIONS THROUGH (*A*) THE PROBOSCIS AND (*B*) THE BRANCHIAL REGION OF THE TRUNK OF *Balanoglossus Kowalewskii* (*B* after SPENGEL).

cop = collar-cœlom.
g = tongue-bar of skeleton.
h = heart.
kd = branchial valve.
kh = branchial portion of œsophagus.
ks = branchial septum.
kp = branchial pore.
lm = longitudinal muscles.
nc = notochord.
nd = dorsal nerve.
nv = ventral nerve.
o = œsophagus.
pc = proboscis-cœlom.
pg = proboscis-gland.
ps = proboscis-vesicle.

In the posterior portion of the proboscis is found a plate of chitinlike material produced into two horns posteriorly, and frequently somewhat hollowed out in front. It is evidently supportive in function, and forms the proboscis-skeleton. In connection with the branchial slits a similar chitinous skeleton is formed (Fig. 276) consisting of a series of transverse bars placed over each septum between adjacent slits. From the middle of each bar a rod (really double) passes down each septum (*sb*), and from the extremities a bar (*tb*) passes into each of the adjacent tonguelike valves, each valve thus possessing a bar from the arch lying in front of it and another from that lying behind it. The septal bars and the tongue bars belonging to each arch are connected by transverse bars (synapticula, *s*) which extend across the valves of the branchial slits.

The digestive tract is practically a straight tube extending from the mouth, situated on the ventral surface of the neck of the proboscis, to the terminal anus. From the dorsal wall of the œsophagus a finger-shaped diverticulum arises, the notochord, which extends forwards into the proboscis; its lumen, in its terminal portion, being practically obliterated by the vacuolization and enlargement of the cells which line it and which are continuous with the endodermal lining of the digestive tract. In the anterior portion of the trunk region the branchial slits already referred to occur, arising as diverticula from the dorso-lateral portions of the intestine (Fig. 275, *B*, *kh*) and eventually opening to the exterior (*kp*). More posteriorly in some species the wall of the intestine is pouched out into sacculations which have been regarded as liver-sacs. In *Balanoglossus* (*Glandiceps*) *hacksi* an accessory intestine occurs, arising in the middle of the liver region from the dorsal surface of the intestine in the form of a tube, which, more posteriorly, opens again into the intestine. It recalls the accessory intestine of certain Annelids, Gephyreans and Echinoderms, but is peculiar in being dorsal in position. In certain species also paired or unpaired communications of the intestine with the exterior have been found, usually arising in the liver region, and opening upon the dorsal surface; their significance is at present unknown.

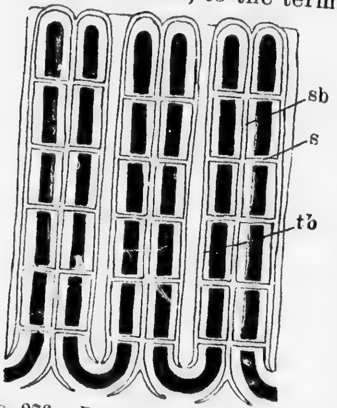


FIG. 276.—DIAGRAM OF THE BRANCHIAL SKELETON OF *Balanoglossus* (after SPENGEL).

s = synapticula.
sb = septal bar.
tb = tongue-bar.

A well-developed nervous system is present in the form of an elongated cord lying in the mid-dorsal line of the collar region, with the ectoderm of which it is in connection at either end, though free throughout the greater portion of its length. It contains in young forms a central lumen, which may be represented in adults by a series of separated cavities and which results from its formation as an invagination of the ectoderm. From this dorsal cord a plexus of nerve-fibres extends all over the surface of the body, lying in the lower layers of the ectoderm and being at certain regions specially developed so as to form nervelike thickenings. One of these surrounds the dorsal and lateral surfaces of the base of the proboscis, being perforated by the proboscis-pore; another occurs at the posterior edge of the collar; while two others occur in the trunk region, one in the dorsal (Fig. 275, *B*, *nd*) and the other (*nv*) in the ventral mid-line, extending the entire length of the trunk. No special optic, olfactory, or auditory organs seem to be developed.

The short canal opening by the proboscis-pore has been regarded as excretory, but the assignment of such a function to it seems questionable. A similar function has been assigned to two short tubes with folded ciliated walls which communicate internally with the cœlom of the collar, and open to the exterior by the collar-pores, situated, one on each side, on the edges of the atrial folds. More definite information is required concerning these organs before they can finally be accepted as excretory; they evidently correspond to the collar-pores of the Pterobranchia.

All the known species of *Balanoglossus* are bisexual, the reproductive organs, ovaries or testes, consisting of simple or branched pouches situated in the trunk, beginning in the brancial region and extending some distance backwards. Each pouch opens to the exterior by a special duct, upon the dorso-lateral portions of the body.

Development of the Enteropneusta.—Some species of *Balanoglossus* (*B. Kowalewskii*) develop directly without the intervention of a larval stage in the life-history, but the majority possess a characteristic free-swimming larva known as the *Tornaria* (Fig. 277). It is a barrel-shaped organism, bulged out slightly at either pole, and possessing a locomotor apparatus in the form of somewhat complicated bands of cilia. One of these surrounds the posterior portion of the body as a simple circular band, while another runs over the anterior portion in an exceedingly tortuous course. It may be considered as consisting of two portions, one præoral in position and the other postoral, the two meeting, however, at the apex of the body in an ectodermal thickening, the apical plate (*a*), which bears two eyes.

The mouth (*M*) opens by a short œsophagus into a capacious stomach (*S*), separated by a perforated partition from the short rectum (*R*), which opens by the terminal anus. In the anterior portion of the body is a saclike structure (*pc*), united to the apical plate by a muscular band and opening to the exterior by a pore (*p*) situated a little to the left of the mid-dorsal line. This sac is the proboscis-cœlom, and the pore the proboscis-pore, and in connection with the sac is a smaller sac, the so-called heart, which becomes the proboscis-vesicle of the adult. At a later stage of development two other pairs of cœlomic sacs (*cc* and *tc*) make their appearance at the sides of the stomach and give rise to the collar and trunk cœlom. The adult form is acquired by the gradual transformation of this larva, there being no sudden metamorphosis.

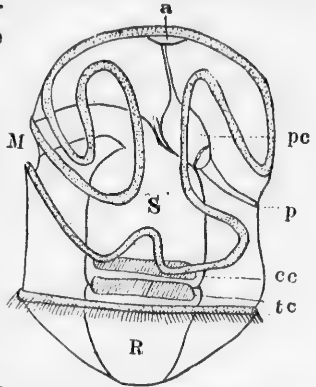


FIG. 277.—TORNARIA LARVA OF *Balanoglossus*.

a = apical plate.
cc = collar-cœlom.
M = mouth.
p = dorsal pore.
pc = proboscis-cœlom.
R = rectum.
S = stomach.
tc = trunk-cœlom.

The Affinities of the Hemichordata.—There seems little room for doubt but that the Pterobranchia and the Enteropneusta are closely related, so many similar and at the same time peculiar structures being found in both groups. Thus, to mention only some of the more striking features, both groups possess a notochord of a similar character, proboscis-pores, collar-pores and branchial slits, and have the body and cœlom divided into three strictly comparable regions. These remarkable similarities can only be explained on the assumption of a common ancestry for both groups.

In many respects, too, the Enteropneusta present similarities to the succeeding group, the Cephalochorda, but a discussion of this relationship may be postponed for the present, and attention called to the suggestive character of the *Tornaria*. Its first describer took it for an Echinoderm larva, and the majority of succeeding authors have been inclined to regard it as indicating affinities with that group. The arrangement of the præoral and postoral ciliated bands, and the occurrence of the proboscis-pore, suggest the Echinoderm larva without doubt, but it must still be regarded as a decidedly open question whether or not these features indicate an affinity. Further information is required both in regard to the ancestry of the Echinoderms and as to the life-histories of the Pterobranchia, before the question can be settled.

Another line of ancestry must also be mentioned, namely, one which leads back to ancestors common to the Hemichordates and the Prosopygia. The similarities of the Pterobranchia to the Polyzoa are striking, there being the same bending of the intestine, similar lophophorelike tentacular structures, and, what is of considerable importance, a dorsally situated nervous system arising as an invagination of the ectoderm. A further point perhaps of some importance may also be mentioned, i.e., the occurrence of three sections in the body-cavity of the Brachiopoda. In following out the line of descent suggested by these similarities, we are, however, quickly brought to a halt by the uncertainty connected with the origin of the Prosopygia, and we are left standing between two lines, one leading back to the Prosopygia and the other to the Echinoderms. Whether or not these two lines converged to common ancestors in pre-Cambrian times cannot be ascertained, and the solution of the problem must be left to future embryological investigations.

II. CLASS **CEPHALOCHORDA.**

The class Cephalochorda contains a single genus, *Amphioxus* (*Branchiostoma*), which is exclusively marine in habitat, being found buried in an upright position in the sand, the anterior end of the body alone showing at the surface.

The body in all species is elongated (Fig. 278) and somewhat flattened from side to side, and bears along the mid-dorsal line an unpaired fin, formed as a fold of the body-wall, and containing a cavity traversed by numerous skeletal rods (see Fig. 279) which serve as a support for the fin. Posteriorly it becomes somewhat higher, and forms a caudal fin surrounding the posterior end of the body, while on the ventral surface two fins run forward a short distance, both these and the caudal fin being supported by fin-rays. Some distance from the hind end of the body on the left side of the caudal fin is situated the anal opening (Fig. 278, *a*), while in front of the anterior end of the paired ventral fin is the atrial pore (p), which leads into a cavity termed the atrium (b). The outer walls of this cavity arise as folds of the sides of the body, termed the epipleural folds, which, increasing in size, fuse together below except at the atrial pore, thus enclosing the atrial cavity (Fig. 279, b), which is lined throughout by ectoderm and surrounds the sides and ventral surface of the anterior two thirds of the body. Anteriorly the cavity is closed by the fusion of the folds with the body-wall in the neighborhood of the larval mouth, but in front of this is a hood-shaped fold which arises independently of the atrial folds and forms the oral hood, at the bottom of which lies the original mouth, the margins of the hood surrounding what may be termed for distinction the adult mouth (Fig. 278, o). These margins are produced into a number of tentacular processes, termed cirrhi, each one of which contains an axial supportive rod borne by a skeletal ring surrounding the adult mouth, and each has its surface raised into numerous sensory papillæ.

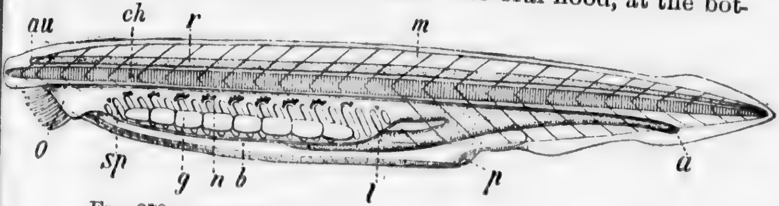


FIG. 278.—*Amphioxus lanceolatus* (after BOVERI from HERTWIG).

a = anus.
au = eye.
b = atrial chamber.
ch = notochord.
g = reproductive organ.
l = liver.
m = muscles.
n = nephridium.
o = mouth.
p = atrial pore.
r = dorsal nerve-cord.
sp = branchial cleft.

The ectoderm is very simple in its character, consisting of a single layer of cells resting below upon a well-developed layer of connective tissue. The arrangement of the cœlomic cavities is by no means simple, however, and may be best understood by considering their mode of development. In a very young embryo a fold may be seen extending along each side of the primitive digestive tract on its dorsal surface. In time these folds are gradually constricted off from the intestine, and at the same time are divided transversely into a number of sacs lying one behind the other, their number increasing as the folds are separated from before backwards from the intestine, until in *A. lanceolatus* there may be as many as sixty-one. These sacs are the primitive mesodermic somites, and the cavities they contain are the primitive cœlomic cavities. At first entirely dorsal in position, the various sacs later on extend ventrally, those of opposite sides meeting below the intestine; and still later the cavities of these ventral extensions fuse to form a continuous cœlom extending the entire length of the body on the ventral surface, and forming what is termed the splanchnocœl. This becomes eventually separated by a layer of connective tissue from the more dorsal portions of the somites, which remain distinct from each other throughout life and are termed the myocœls. The future history of the two portions of the mesoderm thus formed is very different. The walls of the splanchnocœl remain thin, and the cavity well marked (Fig. 279, *co*), but in the myocœls the cells forming the median walls become converted into longitudinal muscle-fibres (*m*) which traverse the entire length of each myocœl, filling it almost completely, and are inserted into plates of connective tissue which develop between the various myocœls and separate them from one another. At the same time each myocœl becomes bent, so that its dorsal portion is directed downwards and forwards and its ventral portion downwards and backwards, each muscle-plate having in a longitudinal section of the body a <-shaped appearance and fitting into the one in front of it. When the epipleural folds develop, both the splanchnocœl and the muscle-plates are continued into them, the muscle-plates lying to the outer side of the splanchnocœl, and their fibres here having for the most part a transverse direction, instead of a longitudinal one, as in their upper portions. Owing to the myocœls being practically obliterated by the muscle-plates, the cœlom of the adult is principally formed of the splanchnocœl, but other spaces also occur which are probably schizocœlic in origin and form various lacunæ throughout the body.

A blood system is present, probably communicating here and there with these lacunæ, and containing a colorless blood in which float numerous colorless amœboid corpuscles. The system consists of a dorsal aorta, single throughout the greater portion of its course, but divided into two trunks over the branchial region of the intestine. It sends off branches to various regions of the body which, after breaking up into capillaries, unite again to form the subintestinal or ventral vein, which, passing forwards till it reaches a point in front of the branchial region, becomes sinuous, and gives off a right and left branch to the lips of the larval mouth (the velum), and a third large vessel on the right side which passes dor-

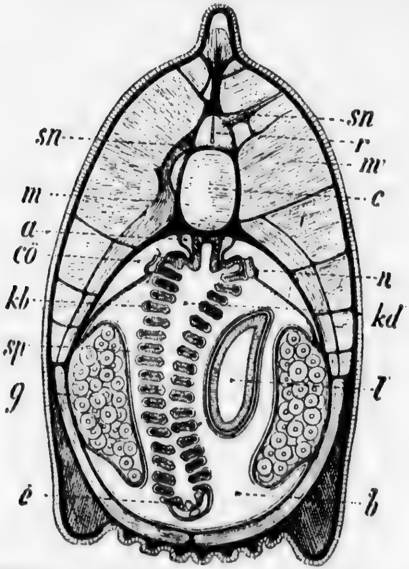


Fig. 279.—Transverse Section through the Branchial Region of *Amphioxus* (after Lankester and Boveri from Hertwig).

a = descending aorta.
b = atrial chamber.
c = notochord.
co = cœlom.
e = hypobranchial groove beneath which is the ascending aorta.
g = reproductive organ.
kb = branchial arches
kd = pharynx.
l = liver.
m = muscles.
n = nephridium.
r = nerve-cord.
sn = nerves.

sally to unite with the right aortic vessel. The blood which passes from the dorsal aorta to the intestine is not, however, returned directly to the ventral vein, but the intestinal capillaries unite to form a vena porta which passes to the liver and there breaks up into a second set of capillaries, these finally emptying through the hepatic vein into the ventral vessel. An hepatic portal system, resembling that found in the Vertebrata, thus occurs in *Amphioxus.* While passing beneath the branchial region of the intestine the ventral vein gives off paired vessels, the branchial arteries, opposite each branchial septum, and these passing dorsalwards in the septum open into the dorsal aortic trunks. There is no definite heart, but certain of the vessels, notably the vena porta and branchial arteries, seem to be contractile.

The notochord (Figs. 278, *ch*, and 279, *c*) has a much more extensive development than in the Hemichorda, since it traverses the entire length of the body. It arises from the dorsal surface of the digestive tract, but early loses all connection with the intestine; and though in early stages it contains traces of a lumen, this quickly disappears, the cells becoming richly vacuolated, so that the notochordal tissue assumes a characteristic appearance. At either end it is pointed, and throughout its entire length it is surrounded by a sheath of dense connective tissue, which is continuous below with the partitions separating the splanchnocœl from the muscle-plates and these from one another. From each side of the dorsal surface of the sheath a longitudinal lamella extends dorsally, the two lamellæ enclosing the central nervous system and being continued above it as a strong neural ridge (Fig. 279).

As has been already stated, the adult mouth is formed by the margins of the oral hood, the original larval mouth lying at the bottom of the oral cavity enclosed by the hood and being surrounded by a circular fold of tissue termed the velum. A short tube leads from the mouth to the branchial or pharyngeal region of the digestive tract, whose walls are here perforated by numerous slits (Fig. 278, *sp*) placing its cavity in communication with the atrium (see Fig. 279). In the adult the slits are elongated and are placed obliquely to the axes of the body; they do not possess a metameric arrangement, but are much more numerous than the muscle-plates of the branchial region of the body, as many as one hundred slits occurring in fully-developed individuals. In the partitions between each pair of slits of the same side of the body skeletal rods occur which unite above with a longitudinal bar lying above the dorsal ends of the slits (Fig. 280). A closer examination shows that alternate bars differ in structure, a condition due to the fact that each pair of slits is primarily derived from a single slit, which becomes divided longitudinally by the growth from its dorsal edge of a tonguelike valve, which eventually fuses with the ventral edge of the slit. The condition of affairs then is almost identical with what obtains in *Balanoglossus*, and, as in that form, the skeletal bars are to be considered as grouped together in threes, although the two bars which in *Balanoglossus* occur in each tongue are fused together (*tb*) in *Amphioxus*, a continuity of the various triads being thus produced. The similarity in the arrangement of the branchial skeleton in the two forms may be seen by comparing Fig. 280 with Fig. 276 (p. 605).

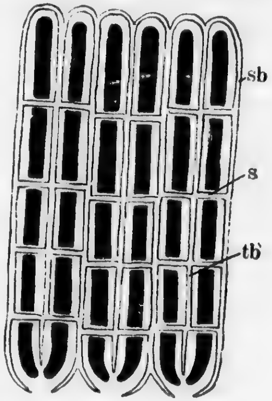


FIG. 280.—DIAGRAM OF THE BRANCHIAL SKELETON OF *Amphioxus* (after SPENGEL).
s = synapticula.
sb = septal bar.
tb = tongue bar.

It follows from this that the actual number of branchial slits in *Amphioxus* is half the apparent number; but even with this reduction the metamerism of the slits does not agree with that of the muscle-plates. In the early stages of development eight pairs of slits are developed which do correspond metamerically with the mesodermic somites, but later additional non-metameric slits are formed, and the original ones are pushed forward at the same time, so that the metameric correspondence is lost.

Blood-vessels occur both in the septa between the primitive slits and in the tongues, and the edges of the slits are ciliated, so that a current of water enters by the mouth, passes through the slits into the atrial cavity, and thence to the exterior by the atrial pore. Along the dorsal and ventral mid-lines of the branchial region is a distinct ciliated groove, the ventral one having projecting from its floor a longitudinal ridge, while ventral to it is a chitinous skeletal plate composed of paired moieties having a metameric arrangement. This ventral or hypopharyngeal groove (Fig. 279, *e*) is termed the endostyle, and from its anterior end a band of ciliated cells passes dorsally on each lateral wall of the pharynx to unite dorsally with the epithelium of the dorsal or hyperpharyngeal groove.

From the digestive tract behind the branchial region a diverticulum, termed the liver (Fig. 278, *l*) arises, and projects forwards, covered of course by the body-wall, into the atrial cavity (Fig. 279, *l*), and behind this the intestine passes straight back to open at the anus (Fig. 278, *a*), situated, as already indicated, upon the left side of the body, some distance from the posterior end.

The nervous system consists of a thick-walled tube (Figs. 278, and 279, *r*) which lies immediately above the notochord and is enclosed by the connective tissue lamellæ which arise from the notochord-sheath. It extends throughout the entire length of the body, tapering rather suddenly at either extremity. Throughout the greater part of its course the lumen is very small, forming the central canal from which a well-marked cleft, the dorsal fissure, extends to the dorsal surface. At the anterior end of the tube, however, the lumen enlarges to form an anterior ventricle (Fig. 281, 1) which has been compared with the anterior of the three primary vesicles of the Vertebrate brain, and behind this the lumen contracts

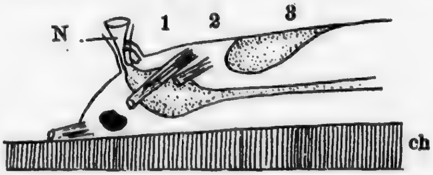


FIG. 281.—DIAGRAM OF THE ANTERIOR PORTION OF THE NERVOUS SYSTEM OF *Amphioxus* (after HATSCHEK).

ch = notochord. *N* = hypophysis.

1, 2, 3 = are placed over the three ventricles.

forming the aqueduct of Sylvius of the mid brain (2), while behind this again an expansion of the dorsal portion of the dorsal fissure forms a *fossa rhomboidalis* (3) similar to that of the Vertebrate hind-brain, the resemblance to the embryonic Vertebrate brain being thus very marked—a resemblance which is increased by the occurrence of a funnel-like extension (*N*) of the anterior ventricle towards the dorsal surface of the body, where it abuts upon a ciliated depression of the ectoderm. This is the remains of a communication of the ventricle with the exterior which exists in the embryo, and has been compared with the hypophysis of the Vertebrate brain, the difference of its position in the latter being due to the flexion of the brain round the anterior end of the notochord.

From the brain region of the nerve-tube three pairs of nerves are given off (Fig. 281), the first and second of which come from the dorsal portion of the brain, while the third pair on each side is double, consisting of a root arising from the dorsal surface of the brain and another arising from the ventral side, a condition which is repeated in the succeeding metamerically-arranged nerves. The dorsal and ventral roots never unite to form a common trunk as in the Vertebrata, nor do the dorsal nerves bear a ganglion, but nevertheless they are sensory in function, while the ventral nerves are motor, supplying only the musculature of the body.

Of sense-organs the papillæ upon the cirrhi and the ciliated depression in connection with the hypophysis have been already mentioned, the latter, on somewhat insufficient grounds, having been supposed to be olfactory in function. In addition to these a pigment-spot, which may represent an exceedingly simple eye, occurs upon the anterior end of the brain, and in the roof of the oral cavity a patch of cells occurs, surrounding a depression lined with columnar cells bearing long refractive hairs. This last structure seems to be a sense-organ of some kind, but its exact function is unknown.

Different structures have from time to time been considered excretory organs. In the first place an excretory function has been assigned to a ciliated tube lying in the wall of the oral cavity on the left side and communicating by a funnel with the cœlom just behind the level of the velum. Secondly, although in all probability they are not nephridia, the "brown canals" may be here mentioned. These lie in the splanchnocœl at about the level of the twenty-seventh muscle-plate in *A. lanceolatus*, and open by wide funnels into the atrium, though it is uncertain whether the inner end lying in the cœlom is perforated. Thirdly, in the pharyngeal region a number of nephridial canals have lately been described. They are situated above the upper ends of the branchial slits (Fig. 282, *nc*), each opening into the atrium opposite a tongue-valve (*np*), and from the short tube which passes inward from this opening an anterior and a posterior branch arises, each of which opens into the cœlomic cavity by a terminal funnel. Between these two funnels three or four others may occur (*nd*), and around the mouth of each funnel are a number of threadlike processes which end in round strongly-refractive cells. That these structures are nephridia seems indicated by their relations to the cœlom and furthermore by the fact that in the neighborhood of each

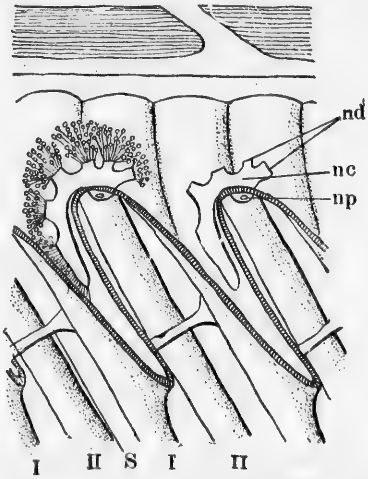


FIG. 282.—EXCRETORY ORGAN OF *Amphioxus* (after BOVERI).

nc = nephridium.
nd = nephridial funnels.
I = branchial septum.
np = nephridial pore.
s = synapticulum.
II = branchial tongue.

of them the branchial blood-vessels form a small plexus which may be regarded as a glomerulus such as occurs in connection with the urinary tubules of the Vertebrate kidney.

Amphioxus is bisexual. The reproductive organs, ovaries or testes (Figs. 278 and 279, *g*), occur in the epipleural folds, and are arranged metamerically, extending in *A. lanceolatus* from the fifteenth to the thirty-fifth or thirty-sixth metamere. They lie at the level of the junction of the lateral longitudinal and the ventral transverse muscles, and are contained within a cœlomic cavity which is a portion of the original myocœls of the segments to which the reproductive masses belong. They lie on the inner surface of the atrial folds, and are covered on their inner surfaces by the thin body-wall, through which the reproductive elements break when mature, falling into the atrium and thence passing to the exterior through the atrial pore. There are no reproductive ducts.

The Affinities of Amphioxus.—The Cephalochorda have usually been considered the most primitive Vertebrates,—as representing, in other words, in a more or less modified condition the stem from which the Vertebrata have descended,—and there are many points of similarity between *Amphioxus* and the larval Lampreys (*Ammocetes*) by which such a view may be supported. The character and origin of the notochord and nervous system, the arrangement of the nerves of the latter, the lateral muscle-plates, the occurrence of an hepatic portal circulation and the character of the early stages of development are all points of similarity which seem explicable only on the supposition of a somewhat close affinity.

On the other hand, resemblances to the Enteropneusta are but slightly less marked. It seems hardly possible that the marvellous similarities in the arrangement of the branchial skeleton should have been acquired independently in the two forms, and the atrial folds of *Amphioxus* may be regarded as the more extensively-developed atrial folds of *Balanoglossus*. *Amphioxus* is undoubtedly much more advanced along the Vertebrate line than *Balanoglossus*, and both are probably more or less widely divergent from the direct line, but the general similarities, such as the occurrence of branchial slits, of an endodermal notochord, and of a dorsally-placed central nervous system, which have led to the association of both forms in the type Protochordata, speak strongly for a community of descent.

The principal difficulty in the way of the acceptance of *Balanoglossus* as the representative of the ancestral forms from which the Vertebrates are descended seems to lie in the supposed necessity for deriving highly-organized metameric forms, such as the Vertebrates, from more lowly but also metameric ancestors, and consequently most authors have sought for indications of Vertebrate ancestry among the Annelida. This difficulty depends upon the interpretation placed upon metamerism and the causes assigned for its origin. If the ideas regarding these points advocated in preceding pages (see pp. 43 and 217) of this book be accepted, the difficulty seems to be practically done away with, since these ideas imply a possibility of the independent origin of metamerism in different groups. And indeed it has already been pointed out that such an independent origin has probably occurred, the metamerism of the Annelids being probably entirely unconnected with the metamerism found in the more highly-organized Platyhelminths (see p. 217).

A full discussion of the intricate problem of the origin of the Vertebrata would be out of place here, but one additional point may be referred to. Difficulties have always stood in the way of an homology of the Vertebrate nervous system with that of the Annelids. In the latter there is a supraœsophageal cerebrum and a ventral chain, while in the former the entire central system is dorsal to the digestive tract. Various theories have been advanced to account for this difference, none of which have, however, proved entirely satisfactory. The acceptance of an ancestry leading back to Hemichordalike forms obviates this difficulty, since in these the slightly differentiated nervous cord is already entirely dorsal, a future extension of it and a metameric arrangement of its elements and branches in correlation with the metamerism of the mesoderm bringing about the Vertebrate condition. Furthermore, the occurrence of a central lumen in the nerve-cord and the mode of its origin are essentially the same in both Vertebrates and Hemichordates, a fact which in itself must be given no little weight in the final determination of the question.

III. CLASS **UROCHORDA**.

The Urochorda, also known as the Tunicata or Ascidians, are, like the other Protochordates, exclusively marine. At first sight they appear to have little resemblance to such a form as *Amphioxus*, the majority of them lacking in the adult condition all trace of a notochord, though a branchial region of the digestive tract is always present. In a few adult forms (Appendicularians, Fig. 285), and in the larvæ of all, a well-developed notochord is present, however, situated in a backward prolongation of the body, resembling in appearance and structure the tail of a young tadpole—an arrangement which has suggested the name applied to the class. In the majority of forms this tail disappears at the close of larval life, and with it the notochord also vanishes. The name Tunicate is derived from the fact that the body is enclosed within an external coat or tunic secreted by the ectoderm of the body and composed, so far as its matrix is concerned, of a substance which is closely related in its chemical characters to vegetable cellulose.

Inasmuch as considerable variation in form occurs in the class, it will be most convenient to describe in detail what may be considered a typical Tunicate, pointing out subsequently the more important modifications which occur.

The simple Ascidians are for the most part ovate in form and usually attached at one end to some support; in the genus *Boltenia*, however, the surface of attachment is at the extremity of an elongated stalk, which at the other end passes into the pyriform body. The test or tunic which encloses the body presents usually towards the free end of the body two openings, through one of which, the branchial aperture, water passes into the interior of the body and is eventually expelled through the second or atrial aperture. This test is composed of a matrix sometimes almost homogeneous, sometimes fibrillar (*Cynthia*), and of varying consistency, secreted by the ectoderm. It contains scattered through it numerous cells, which have recently been shown to be mesodermal in origin and to migrate into the test after it has reached a certain thickness. They may remain amœboid in shape or may develop vacuoles, becoming thereby swollen into bladderlike structures, or may become the seat of pigment-depositions, or, finally, may secrete spicules of carbonate of lime.

Extending through the test are numerous branching tubes which communicate with the blood-vessels of the body. They arise as outgrowths of the blood-vessels and push the body-wall before them, being therefore lined externally by ectoderm, beneath which is a layer of connective tissue, and each is separated into two compartments by a longitudinal partition which does not, however, extend into the bulblike enlargement with which each branch ends, the two compartments thus communicating in the bulb and allowing the blood to circulate.

The shape of the body conforms to that of the test, and opposite the branchial and atrial apertures of the latter is drawn out into two tubular processes, the branchial and atrial siphons, in whose walls circular muscles are developed to serve as sphincters of the openings. The branchial siphon opens posteriorly into the branchial region of the digestive tract, the opening being known as the mouth, and usually being surrounded by a number of tentacles (Fig. 283) which arch over it. The atrial siphon, on the other hand, does not open into the body proper but into a cavity, lined probably

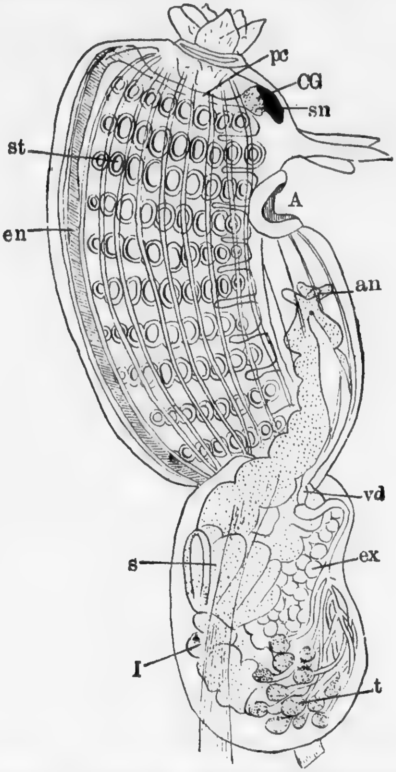


FIG. 283.—FIGURE OF A TUNICATE, *Heterotrema*, REMOVED FROM THE TEST (after FIEDLER).

A = atrial pore.
an = anus.
CG = cerebral ganglion.
en = endostyle.
ex = excretory organs.
I = intestine.
pc = peripharyngeal ciliated band.
s = stomach.
sn = subneural gland.
st = branchial stigma.
t = testis.
vd = vas deferens.

with ectoderm, which almost completely surrounds the body, being wanting only along the ventral wall and at the extreme anterior and posterior ends. This cavity is the atrium and its walls are termed the mantle. It is comparable to the atrial cavity of *Amphioxus*, but has a somewhat more extensive development and arises in the larva as a pair of dorsally-situated invaginations of the body-wall which, gradually increasing in size, enclose the greater portion of the body, and their openings, gradually approximating, finally fuse to form the atrial aperture (Fig. 283, *A*), the dorsal partition between them at the same time disappearing, so that the two cavities become continuous.

The external surface of both the mantle and the body proper is covered with ectoderm, and rests below upon a layer of mesodermal connective tissue which contains muscle-fibres. The cœlomic cavity consists of a number of lacunar spaces which have, especially in the walls of the branchial region, a more or less definite arrangement and serve as blood-vessels. In a somewhat distinct space near the hind end of the body is situated a tubular heart, whose walls are formed of a single layer of cells, the inner ends of which are converted into muscle-fibres. The contractions of the heart are wavelike, starting from one end and passing gradually though rather quickly towards the other; but a remarkable peculiarity is that after a certain number of beats, at each of which the contraction-wave begins at one end, its course is reversed, and for a similar number of beats it begins at the other end. This change takes place with a certain amount of rhythm, and at each change the course of the blood through a portion at least of the body is reversed. At each end the heart opens into a large lacuna, one of which runs along the ventral mid-line of the branchial sac, while the other, giving off lacunar branches to the intestine and test, runs along the dorsal mid-line of the same region, smaller lacunæ, traversing the branchial bars, uniting the two vessels. The blood-plasma is colorless and contains amœboid corpuscles which are also usually colorless, though a few colored ones, resembling the pigmented cells of the test, are frequently found.

The mouth opens into a capacious pharyngeal or branchial sac whose walls are perforated by numerous slits or pores termed stigmata (Fig. 283, *st*), arranged in transverse or spiral rows. The bars separating the stigmata enclose lacunæ which place the ventral and dorsal branchial lacunæ in communication so that the walls of the sac are richly supplied with blood, opportunities for its aeration being provided by currents of water drawn by the cilia which border each stigma through the mouth and out into the atrial cavity, whence it escapes by the atrial aperture. The transverse bars which separate the rows of stigmata are generally stouter than the longitudinal ones, and in most species there is a second series of longitudinal bars lying on the inner surface of the sac, less numerous than the bars which separate adjacent stigmata, united with each transverse bar by a short connecting branch, and bearing opposite each junction a hollow papilla which projects into the cavity of the branchial sac. Running along the entire ventral mid-line of the sac is a ciliated groove (Fig. 283, *En*) bounded on each side by a distinct longitudinal ridge. This is the endostyle, comparable to that of *Amphioxus*, and from its anterior end a band of ciliated cells (*pc*) passes dorsally on each side of the pharyngeal wall to unite in the dorsal mid-line. In front of these bands another pair running parallel to them is usually found, the two pairs forming the peripharyngeal ciliated bands. From the dorsal point of union of the two posterior bands a ridge, the dorsal lamina, extends backwards in the dorsal mid-line of the branchial sac, and in many species (Fig. 283) is produced into a number of processes succeeding one another at intervals, and projecting into the branchial cavity; these are termed the dorsal languets.

The remaining portions of the digestive tract is in the simple Ascidians generally situated in the mantle on the left side of the body, owing to the enormous development of the branchial sac, but in other forms it constitutes a part of a visceral mass lying immediately below the posterior end of the sac. The œsophagus, beginning at the lower end of the sac, forms a short tube which opens into a fusiform stomach, from the further end of which the intestine (*I*) arises. This is generally bent twice upon itself, forming thus two loops, and ends in a straight piece, the rectum, which opens by the anus (*an*) into the atrial cavity. A thickening occurs along the entire length of the inner surface of the intestinal wall, forming the typhlosole, and a number of branched tubules opening into the stomach (*s*) represent a so-called "liver" or digestive gland.

The nervous system consists of a single ganglionic mass (*ca*) lying on the dorsal side of the body near the anterior end and giving off nerves both anteriorly and posteriorly. Immediately below it is a glandular structure, the subneural gland (*sn*), from which a duct passes forwards to open into the anterior part of the branchial sac, at the base of a well-marked papilla which may possibly be sensory in function. The gland, from its relation to the nervous system and the branchial sac, has been compared to the pituitary body (hypophysis cerebri) of the Vertebrates.

Sense-organs are but slightly developed, pigment-spots situated in the neighborhood of the branchial and atrial apertures perhaps representing rudimentary eyes, while sensory functions have been attributed to the tentacles, the dorsal languets, and the papilla at the opening of the duct of the subneural gland.

An excretory function has been assigned to the subneural gland, but in addition to this there are found in the visceral mass a number of spherical bodies (*ex*) without ducts, in whose cells concretions of uric acid are found. These seem to represent excretory organs, the waste material instead, however, of being passed out from the body is stored up in the cells of the organs—a condition recalling what is found in some Echinoderms and, to a certain extent, the arrangement in the Ectoproctous Polyzoa.

The Tunicates are for the most part hermaphrodites. The ovary is a ramified structure lying in the loop of the intestine, and contains a cavity lined with a germinal epithelium. An oviduct is continuous with the ovary and leads towards the atrial cavity, opening into it in close proximity to the anus. The testes (Fig. 283, *t*) are numerous spherical bodies, also situated in the visceral mass, each portion being provided with a duct which joins with others to form the single vas deferens (*vd*), opening into the atrial cavity near the opening of the oviduct.

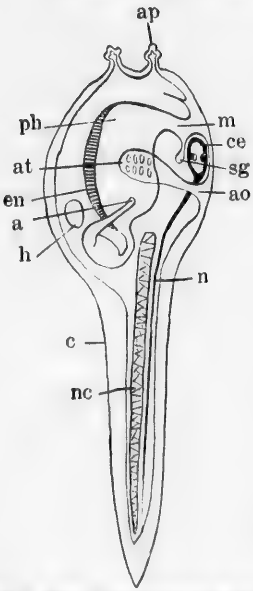


Fig. 284.—Diagram of the Tadpole Larva of a Tunicate.

a = anus.
ao = atrial orifice.
ap = adhesive papilla.
at = atrial cavity.
c = cellulose test.
ce = brain.
en = endostyle.
h = heart.
m = mouth.
n = nerve
nc = notochord.
ph = pharynx.
sg = subneural gland.

On account of the larval characters being more important than the adult in indicating the affinities of the Tunicates and in justifying the term Urochorda applied to the class, it seems convenient to depart from the usual arrangement and consider the development of the simple Ascidians here, before passing on to a description of the various orders.

Development of the Simple Ascidians.—For an account of the early development reference must be made to embryological text-books, the present description being confined to the larva and the changes it undergoes in transforming to the adult. Suffice it to say that the early stages resemble very closely those of *Amphioxus*, and they result in the formation of a remarkable structure usually known as the Ascidian tadpole, a term which indicates its general appearance. This larva is a free-swimming organism and consists (Fig. 284) of an anterior somewhat globular portion, the body, and a posterior flattened region, the tail. The entire body is enclosed within a continuous case, the test (*c*), which, in the tail region, is elevated into a dorsal and ventral ridge, serving as fins. Upon the anterior end of the body are papillæ (*ap*) which serve for fixation when the larval life is completed, while in the interior of the body region indications of the various adult organs may be seen. Certain interesting modifications of these are, however, to be noticed; the atrial cavity (*at*) is yet quite small and the anus (*a*) may or may not communicate with it, while the mouth (*m*) is not functional, owing to the test being continuous over it. The nervous system is the most remarkable structure, however, consisting of a large anterior saclike structure, the brain (*ce*), into the cavity of which two sense-organs project. Upon the dorsal wall is the eye, consisting of a cup-shaped group of cells whose inner ends are pigmented, the hollow of the cup being occupied by a lens above which is a membrane, the so-called cornea. Projecting dorsally from the ventral wall is the otolith, consisting of a pear-shaped cell bearing a cap of pigment, its smaller end extending between the cells of the lower wall of the brain, which in its neighborhood are provided with stiff cells forming a crista acustica.

Posteriorly the brain is prolonged into a thick-walled tube (*n*) which extends back almost to the tip of the tail, to the muscles of which it sends off nerves. Beneath the nerve-tube, throughout nearly its entire length, lies a notochord (*nc*) which serves as a skeletal support to the tail, and on each side of it is a plate of longitudinal muscle-fibres.

By means of energetic lateral movements of the tail this larva swims about for some time, but when about to transform itself into the adult it fastens to some solid object by one of the adhesive papillæ. The tail with its nervous system, muscles, and notochord then undergoes degeneration and is completely absorbed, the portion of the test covering it being thrown off, and a rotation of the body takes place so that the mouth comes to lie at the opposite end of the body from the point of fixation. The branchial and atrial apertures form, and the anterior saclike brain collapses, the sense-organs degenerate, and the adult brain is gradually developed. The extension of the atrium and the development of additional stigmata complete the acquisition of the adult characteristics.

It will be seen from this, then, that the larvæ are of great importance in estimating the systematic position and the affinities of the Urochorda, and that the adults, except in the *Appendicularia*, in which the tail and the free-swimming habit are persistent, are to be regarded as degenerate. Several orders of Tunicates may be recognized.

1. Order **Larvacea.**

To this order belongs the genus *Appendicularia* which has already been several times mentioned. It is throughout life free-swimming and retains the larval tail, greatly resembling in general appearance a tadpole larva. It secretes an extensive test which is gelatinous in consistency and is but loosely attached to the body, being frequently thrown off shortly after its formation. The body (Fig. 285) is comparatively small, the tail being attached to its ventral surface, while its posterior extremity is somewhat enlarged and contains the reproductive organs (*ov* and *h*). The branchial sac has but a single pair of stigmata (*s*) which open to the exterior by a pair of funnel-like tubes situated behind the anus. This arrangement represents exactly a condition present in the larvæ of other Tunicates, two stigmata first forming and the atrial sac arising as two separate invaginations of the body-wall into which the primary stigmata open, the invaginations only

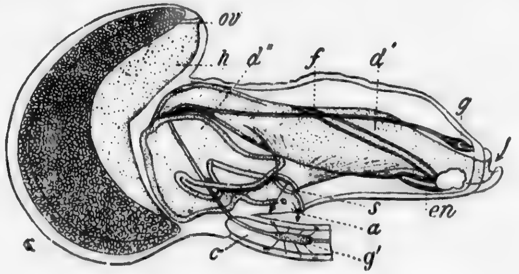


FIG. 285.—AN APPENDICULARIAN, *Oikopleura cophocerca* (after Fol from HERTWIG).

a = anus.
c = notochord.
d' = pharynx.
d'' = stomach.
en = endostyle.
f = ciliated groove.
g = brain with auditory vesicle.
g' = first ganglion of tail.
h = testis.
ov = ovary.
s = branchial cleft.

later fusing to form the extensive atrium. The endostyle (*en*) is very short, and the nervous system is constructed upon the larval plan, though the brain (*g*) is not the sensory sac so characteristic of the larva. It is more ganglionlike and sends off branches to an otocyst lying in its neighborhood, and also gives rise to a tubular prolongation opening into the terminal portion of the branchial sac. Pigment-spots, probably representing rudimentary eyes, are also present, and from the posterior end of the brain a tubular nerve-cord arises which passes backwards and downwards into the tail, which it traverses, dilating at intervals into ganglia (*g'*). The notochord (*c*) lies below the caudal nervous system, and on each side of it are the lateral muscles of the tail, which show no indications of metameric segmentation.

2. Order **Ascidiaceæ.**

The members of this order present the structural features which have been described as typical for the class. Many forms possess the power of non-sexual reproduction by budding, colonies being thus produced some of which may be free-swimming, the simple forms, however, being always fixed. They differ from the Larvaceæ chiefly in the absence of the tail in the adult and in the large development of the branchial sac and the numerous stigmata.

Owing to the complexities produced by the methods of budding it is customary to divide the order into subordinate groups.

1. Suborder *Ascidiæ simplices.*

The simple Ascidians agree with the description given as typical and do not require any further notice here, except to mention the fact that there are included within the suborder a few genera which reproduce by budding, e.g. *Clavellina* and *Perophora.* The formation of new individuals takes place in these cases from stolonlike outgrowths of the parent form, and each bud remains seated upon the stolon surrounded by its own test. The stolon (Fig. 286) arises from the lower portion of the body of the parent and pushes before it a portion of the test; the cavity it contains is continuous with the body-cœlom and is therefore lined by mesoderm, and is divided into two compartments by a longitudinal partition which may be traced back to its origin from the posterior wall of the branchial sac of the original individual. Since ectodermal tissue lies between the mesoderm and the inner surface of the test, the stolon contains portions of all three germ-layers, and a portion of each passes into each bud (*b*) as it arises. The first indication of a bud is a slight wartlike elevation of the wall of the stolon which increases in size, its cavity being a diverticulum of the stolon-cœlom. Into the elevation a process (*en*) of the endodermal stolon-partition extends, and, forming a hollow saclike body, gives rise to the digestive tract of the bud. The various layers give rise to their respective organs with one exception, and that is that the atrial walls, the mantle, arise from the endodermal branchial sac as diverticula which unite together, the atrial cavity being thus lined throughout with endoderm. Such anomalies are not infrequent in the Urochorda, and indicate a necessity for further study of the nature of the germ-layers in these forms.

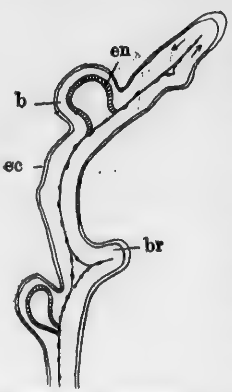


FIG. 286.—PORTION OF A STOLON OF *Perophora* (after KOWALEWSKY from KORSCHELT and HEIDER).
b = bud.
br = branch of stolon.
ec = ectoderm.
en = endoderm.

The simple non-budding forms are quite numerous. Common genera are *Molgula*, *Cynthia* in which the test has a leathery consistency owing to the fibrillar character of the matrix, and *Boltenia*, a stalked form.

2. Suborder *Ascidiæ compositæ*.

All the members of this order reproduce by budding in some form or other, and differ from such forms as *Clavellina* in that all the individuals remain imbedded in a common test whether or not they remain in organic connection with one another. The group seems to be a somewhat composite one, and it is probable that it is an aggregation of forms with quite distinct derivations. The varieties of budding which are found are quite numerous. In some cases it closely resembles that of *Clavellina*, some species of *Distaplia*, for example, possessing a short stolon, essentially similar to that of the former genus, from which buds arise which, however, early separate from the stolon and remain imbedded in the thick test of the parent, a repetition of this process through several generations leading to the formation of massive colonies.

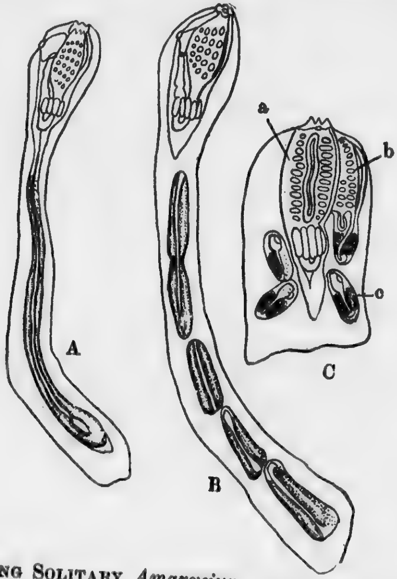


Fig. 287.—*A*, Young Solitary *Amarœcium* developed from Egg; *B*, a slightly Older Form, in which the Postabdomen is segmented; *C*, the Non-sexually produced Forms migrating towards the Surface of the Test (after Kowalewsky from Korschelt and Heider).

a = parent individual. *b* = bud which has reached the surface.
c = migrating buds.

In *Amarœcium* the arrangement is a little different, but can readily be traced back to the stolon form. The posterior end of the body in budding forms is continued backwards as a long postabdomen (Fig. 287, *A*), having a structure similar to the stolon of *Clavellina*, but instead of giving off buds the stolon segments into a number of parts (Fig. 287, *B*) which, separating, rise through the thick test of the parent (Fig. 287, *C*) until they reach the surface, and develop to complete individuals, in which the process may be repeated. *Amarœcium* thus forms massive colonies consisting of a number of quite separate individuals all imbedded in a common test, and all directly or indirectly the result of the budding of a single individual developed by the sexual method.

In other forms, however, the stolon is practically suppressed and the buds arise directly from the body of the parent. This is the case in *Didemnum* and *Tridemnum*, for instance, peculiar complications being also introduced into the process. In the latter form the daughter individual arises as two buds which later fuse. One arises from the upper end of the œsophagus and gives rise to the intestine and neighboring organs in the bud, while the other, arising from the branchial sac, gives rise to that structure, the atrium, and terminal portion of intestine. Usually the two buds arise simultaneously, but occasionally one may fail, the result being the production of half individuals which remain united with the parent, producing double monsters; and since either

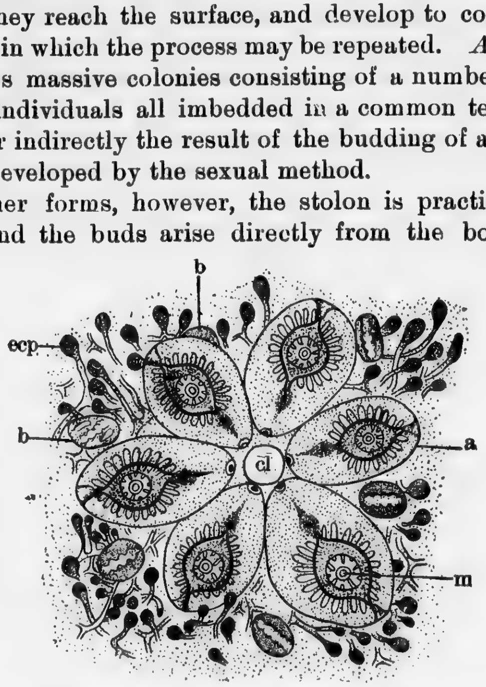


FIG. 288.—A SYSTEM OF SIX INDIVIDUALS FROM A COMPOUND COLONY OF *Botryllus* (after OKA).

a = adult individual.
b = bud.
cl = common cloaca.
ecp = ectodermal processes extending into test from each individual.
m = mouth of one of the individuals.

bud may fail, these monsters may have either a double branchial sac, atrium, and rectum, or a double digestive tract, heart, and other organs of the visceral mass. If, however, both develop simultaneously, in the course of time the perfect daughter form separates from the parent. In *Botryllus* (Fig. 288) but a single bud (*b*) arises from each individual of the colony, developing on one side of the body in the region of the branchial sac, early separating from the parent except for a slight stalklike union. After the formation of the daughter individuals the parent forms die, and so a succession of generations occurs, the various individuals of each generation being arranged in a circle around a common cloaca (*cl*) into which the atrial aperture of each opens.

The origin of a colony of *Botryllus* takes place as follows: An individual developing from an egg fastens itself and gives rise to a single bud, which remains imbedded in the test of the parent, which, on its part, dies and disappears. The individual of this second generation gives rise to two individuals of the third generation and then likewise dies, while each of the members of the third generation gives rise to two more members of a fourth generation and degenerates. The four individuals so formed arrange themselves so that they radiate from a common point at which a depression of the test occurs, forming the cloaca. New generations then succeed each other, the parents of each generation in turn degenerating, and so the colony extends, and some of the individuals failing to form a connection with the original cloaca become centres for a new radiating colony, still, however, imbedded in the common test.

3. Suborder *Pyrosomidæ*.

In this order there is but a single genus, *Pyrosoma*, which includes floating pelagic colonies having the shape of a cylinder closed at one end, the individuals composing the colonies being enclosed in a common test and arranged radially around the central cavity or cloaca into which their atrial apertures open, the branchial apertures opening on the exterior of the cylinder. Each individual resembles in structure a simple Ascidian, the principal difference being that the atrial aperture, as in *Botryllus*, is at the posterior end of the body, and that each individual has the power of reproducing by budding and so assisting in the further growth of the colony, the parent forms not, however, degenerating after giving rise to buds, as in *Botryllus*. The buds arise from the branchial sacs behind the endostyle, and, on separating from the parents, place themselves between them and the opening of the common cloaca, so that the oldest members of the colony lie at the closed end of the cylinder. On each side of the branchial sac of each individual near the anterior end, or more precisely near the peripharyngeal ciliated bands, is a mass of cells which are brightly phosphorescent, the entire colony, which may reach a length of over a metre, emitting a brilliant light when stimulated.

The development of *Pyrosoma* is exceedingly interesting inasmuch as it presents an alternation of generations. From the embryo which develops from the egg at a very early stage a stolon develops (Fig. 289), containing a prolongation of what corresponds to the embryonic branchial sac and also of the embryonic mesoderm. The embryo itself never reaches a full development and is termed the *Cyathozooid*, serving to supply the individuals developed from the stolon with nourishment until they have reached a certain stage of development. This it is able to do on account of the ovum being plentifully supplied with yolk, which the Cyathozooid gradually absorbs. The stolon at an early stage divides into

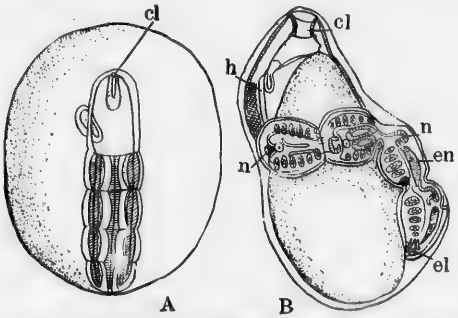


FIG. 289.—LARVAL BUDDING OF *Pyrosoma*. *A*, embryo divided into the cyathozooid and four ascidiozooids; *B*, later stage showing the ascidiozooids twisting to form the circle of four primary individuals (after KOWALEWSKY).

cl = cloaca.
en = endostyle.
el = elæoblast.
h = heart.
n = nerve-ganglion of ascidiozooid.

four parts (Fig. 289, *A*), which arrange themselves in a circle around the Cyathozooid (Fig. 289, *B*), being enclosed with it in a common test, and develop eventually into the four primary individuals or *Ascidiozooids*, which occupy the closed end of the cylindrical colony. As they develop the Cyathozooid degenerates and finally completely disappears, the cloacal cavity of the colony arising, as in *Botryllus*, as a depression of the test, which grows deeper and deeper as new individuals arise by budding.

The entire process shows a marked similarity to what occurs in *Botryllus*, the principal differences being that the Cyathozooid, which represents the first generation of *Botryllus*, buds while yet in an embryonic condition, and that it alone degenerates, the parents of succeeding generations persisting and forming parts of the fully-developed colony. In each Ascidiozooid there occurs behind the branchial sac a pair of peculiar masses of cells termed the *elæoblast* (Fig. 289, *B*, *el*), whose function is uncertain, though it has been suggested that they may represent the rudimentary larval tail.

3. Order **Thaliacea.**

The Thaliacea are with a single exception pelagic organisms, and present a life-history complicated by the occurrence of an alternation of generations. In the genus *Salpa* (Fig. 290) a well-developed test is present, and the musculature of the mantle is arranged in bands which do not quite surround the body and furthermore show a tendency to unite together on the dorsal surface of the body. At one end of the body is a large branchial aperture (*m*) leading into a branchial sac, in the floor of which is the endostyle (*en*), while in its roof is a ridge, the dorsal lamina, which anteriorly is produced into a single languet projecting into the interior of the sac. On each side of the dorsal lamina is a large opening which represents an enormous stigma and communicates with the atrial cavity, whose aperture is situated at the posterior end of the body. The intestine and the other viscera are grouped together to form a small mass termed the nucleus (*nu*) lying behind the branchial sac and ventrally, though in some forms the intestine is more elongated and projects somewhat from the nucleus. The nervous system (*n*) has its usual form and position; it has in connection with it three pigmented spots probably representing eyes, and the subneural gland is present as usual.

Each species of *Salpa*, however, presents two distinct forms (*A* and *B*), differing in shape and in the number of the muscle-bands which are found in the mantle and having likewise a different origin. In the sexual form (*A*) reproductive organs are developed, the ovary usually containing but a single ovum. This when fertilized (*em*) is passed into the atrial cavity, the follicle-cells with which it is surrounded forming an adhesion to the wall of the cavity, and later modifying to form a structure recalling the placenta of the Mammalian Vertebrates by which nourishment is conveyed from the parent to the embryo. As the result of the development of this ovum the non-sexual form (*B*) is produced, which is characterized not only by its general form, but also by the possession of a stolon (*st*) arising from the branchial sac just

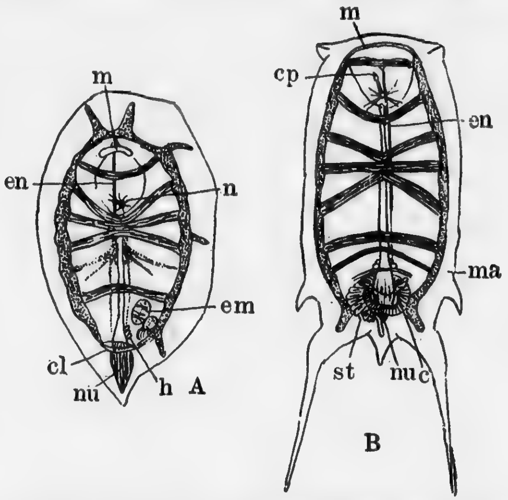


FIG. 290.—*A*, *Salpa mucronata*, THE SEXUAL FORM, AND *B*, *Salpa democratica*, THE NON-SEXUAL FORM OF *Salpa democratica-mucronata* (after CLAUS).

c, *cl* = cloaca.
cp = ciliated pit.
em = embryo.
en = endostyle.
h = heart.
m = branchial pore (mouth).
ma = test.
n = nerve-ganglion.
nu = nucleus.
st = stolon.

behind the posterior end of the endostyle. This stolon eventually divides into a large number of parts, each of which, after undergoing certain somewhat complicated shiftings of position on the stolon, develops into the sexual individual. The terminal portions of the stolon with the maturer individuals from time to time break off and float about, forming what are termed the Salpa-chains, and the constituent individuals of the chain, the sexual individuals, becoming mature either while still united with their fellows or after separation from them, start again the life-cycle which may be represented by the following scheme:

Ovum = Solitary Salpa——Chain Salpa——Ovum.
(Non-sexual) (Sexual)

In another genus belonging to the order, *Doliolum* (Fig. 291), the process is somewhat more complicated. The members of this genus are barrel-shaped forms, the wide branchial aperture being situated at one end and the atrial aperture at the other; the stigmata are fairly numerous and arranged in two lateral rows, and the mantle muscle-bands form complete circles around the body, resembling the hoops of the barrel. From the ovum there develops a peculiarly-constructed tailed embryo, which, with the loss of the tail, becomes converted into the non-sexual form (Fig. 291, *A*) characterized by the possession of nine circular muscle-bands, an otocyst (*ot*) situated some distance from the nervous system on the side of the body, a ventral stolon (*st*), and a dorsal posteriorly-directed process (*dp*). From the stolon a number of buds are produced, which, at an early stage, separate from the stolon and migrate to the dorsal process to which they attach themselves, the migration being accomplished, it is said, by means of amœboid cells, probably cells of the test, which attach themselves in pairs to the base of each bud and serve to convey it to the dorsal process. Upon this process the buds arrange themselves in three rows, the individuals of the lateral rows developing into forms quite different from those resulting from the development of the buds of the median row. The lateral buds when freely developed are characterized by the possession of a large branchial aperture, which occupies almost the entire length of one side of the body and leads into a branchial sac whose stigmata open directly to the exterior, the atrial cavity disappearing during the course of development. The intestine is well developed, but the muscles are but slightly indicated, while the reproductive organs, rudiments of which were present in the young buds, completely atrophy during the process of development. These buds are incapable of leading a free existence, serving only as nutritive and respiratory individuals for the median buds, as well as for the parent, whose digestive tract degenerates, its muscle-bands and nervous system at the same time under-

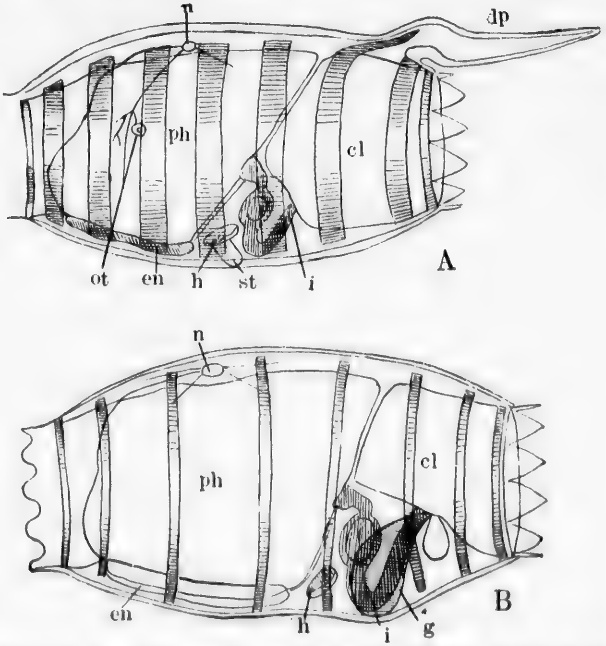


FIG. 291.—*A*, THE NON-SEXUAL, AND *B*, THE SEXUAL, FORM OF *Doliolum* (after ULIANIN).

cl = cloaca.
dp = dorsal process.
en = endostyle.
g = reproductive organ.
h = heart.
i = intestine.
n = nerve-ganglion.
ot = otocyst.
ph = pharynx.
st = stolon.

going enlargement, so that it serves eventually as a locomotor individual for the entire aggregation of individuals.

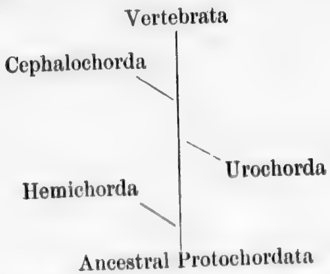
With regard to the median buds differences of opinion occur. Certain of them, or according to one authority all, being set free, develop into forms possessing but eight muscle-bands, no otocyst or dorsal process, but having a ventral median process upon which buds are found. It is in regard to the origin of these buds that the difference of opinion exists. According to one view they are produced from the ventral process which is regarded as a stolon and represent a third generation, while according to the other view they are certain members of the median row of the second generation, the forms bearing them being as it were their sisters and serving as nurses for them. Whatever may be their origin, however, the buds eventually are transformed into sexual individuals (Fig. 291, *B*) with which the life-cycle was commenced. The two views as to the cycle in *Doliolum* may be schematically represented thus:

Ovum = non-sexual form
- Nutritive individuals
- Nurses — Sexual forms—Ova
- Nutritive individuals

Ovum = non-sexual form
- Nutritive individuals
- Nurses
- Sexual forms — Ova
- Nutritive individuals

Mention should be made of the genus *Octacnemus*, a deep-sea form belonging to this order which is apparently attached by a pedicle to foreign bodies. The body proper is flattened and disklike, its margins being prolonged into eight tapering processes. The mouth lies on the surface of the disk and leads into a shallow branchial sac. The atrium is comparatively large, and the intestine and viscera are, as in *Salpa*, massed together in the form of a nucleus. Nothing is as yet known as to the life-history of this form.

Affinities of the Urochorda.—There seems little room for doubt but that the Urochorda are related to *Amphioxus*. The two groups present too many common structural features to allow of their being regarded as distinct types, but at the same time it is noticeable that the relationship is through the larval Tunicates rather than through the adults. These latter are degenerated forms, the entire group forming a degenerate offset from the main line of evolution represented by the Protochordata and leading to the Vertebrata. The early stages of development of the simple Tunicates (see text-books of embryology) are so very similar to those of *Amphioxus* that it must be concluded that the evolution of the Urochorda and Cephalochorda proceeded for some distance along similar lines, and the general affinities of the Protochordata may possibly be indicated by a scheme thus :



Taking the larval Tunicates as a basis for comparison, we find as features common to them and *Amphioxus* a dorsal nervous system arising as an invagination of the ectoderm and extending the entire length of the body ; in the anterior portion the lumen of the nerve-cord expands to form a brain which in *Amphioxus* opens in early stages to the exterior and in the Tunicates into the anterior portion of the branchial sac, i.e., the ectodermal portion, the canal of communication in the latter forms losing in later stages its connection with the brain and forming the subneural gland. An atrial cavity occurs in both, which, though arising in a somewhat different manner in the two groups, nevertheless seems quite homologous, and homologies have also been pointed out between the primary gill-slits. The increased number of stigmata and their arrangement in the Tunicates is a secondary character resulting probably from the sessile existence ; and the development of the test and the limitation of the notochord to the tail are also probably secondary characters. The resemblances are important ones, and when taken into consideration with the embryonic development point very strongly to a close affinity.

As regards the relationships of the various groups of Urochorda to one another considerable difference of opinion exists. The Appendicularians, which at first sight seem to be the most primitive of all the orders, present certain remarkable peculiarities, such as the separate openings of the atrial cavities and the anus, and some authors are inclined to regard them not as primitive forms, but as sexually-mature larvæ of sessile forms in which a test had already developed and degeneration far advanced. As regards the remaining forms the simple Ascidians seem to be the most primitive, the composite forms being derived from them by the acquisition of nonsexual reproduction. The composite forms, however, seem really to represent several groups originating independently, all the members not having descended from an ancestral simple form, but some from one ancestor and others from another, and so on. The Thaliacea, finally, have probably been derived from composite forms, *Pyrosoma* showing certain affinities in its budding to *Salpa*, the fact of some individuals being solitary not necessarily indicating a primitive character, since in the composite forms no organic union exists between the various individuals of the colony when they have reached maturity, so that the so-called colonies are rather aggregations than colonies, and the forms more properly termed social than colonial or even composite.

SUBKINGDOM METAZOA.

TYPE PROTOCHORDATA.

I. Class HEMICHORDA.—Body divided into three distinct regions; notochord a small fingerlike diverticulum projecting forwards from anterior portion of digestive tract, with which it retains connection.

- 1. Order *Pterobranchia*. — Sessile colonial forms, secreting a "house"; intestine bent upon itself; collar region with lophophorelike, tentacle-bearing processes. *Cephalodiscus*, *Rhabdopleura*.
- 2. Order *Enteropneusta*.—Free forms not forming colonies; not secreting a test; intestine straight; collar region without lophophorelike processes. *Balanoglossus*.

II. Class CEPHALOCHORDA.—Free forms, not pelagic; not secreting a test; body not divided into three distinct regions, with numerous metameres; notochord completely separated from digestive tract and traversing the entire length of the body. *Amphioxus*.

III. Class UROCHORDA.—Sessile or free pelagic forms; secreting a test; body in adult not divided into three distinct regions and showing no indications of metamerism; notochord usually wanting in adult, present in tail-region of larvæ and entirely separate from digestive tract.

- 1. Order *Larvacea*.—Retaining the larval tail with notochord; free simple pelagic forms. *Appendicularia*.
- 2. Order *Ascidiaceæ*.—Simple and sessile or colonial and occasionally pelagic; tail and notochord wanting in adult.
    - 1. Suborder *Ascidiæ simplices*.—Simple sessile forms or else budding from stolons and forming somewhat straggling colonies, the various individuals not enclosed in a common test. Simple forms, *Molgula*, *Cynthia*, *Boltenia*; Colonial, *Clavellina*, *Perophora*.
    - 2. Suborder *Ascidiæ compositæ*.—Colonial forms, the various individuals embedded in a common test; if the various individuals open into a common cloaca the colony is not pelagic. *Amaræcium*, *Didemnum*, *Tridemnum*, *Distaplia*, *Botryllus*.

3. Suborder *Pyrosomidæ.*—Colonial forms, the various individuals imbedded in a common test, and opening into a common cloaca; pelagic; with alternation of generations. *Pyrosoma.*

3. Order *Thaliacea.*—Simple pelagic forms, with alternation of generations. *Salpa*, *Doliolum*, *Octacnemus.*

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Group
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ACARIN
Acervul
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Acmæa,
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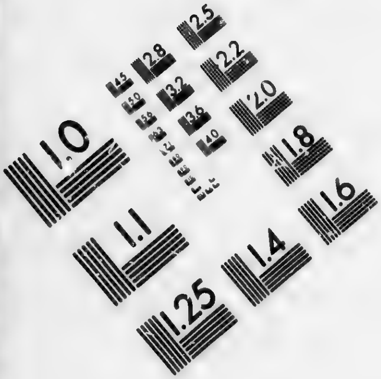

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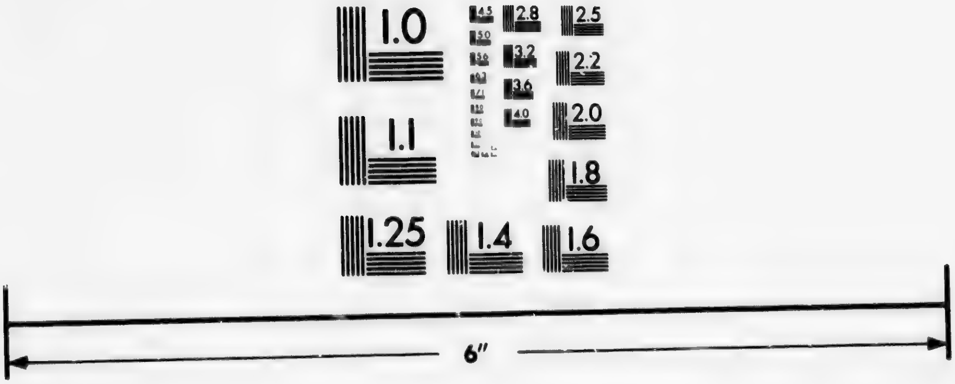
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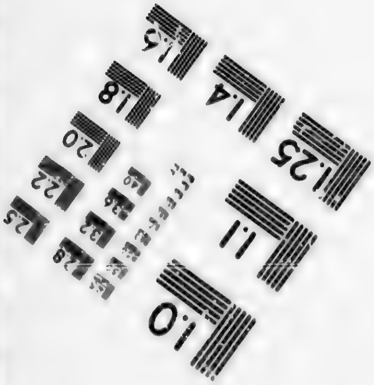
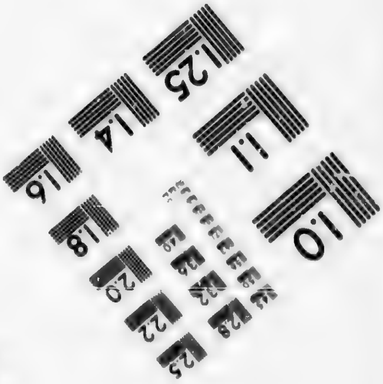
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